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Recovery Potential Assessment for the American Eel (*Anguilla rostrata*) for Eastern Canada: Recovery Potential Assessment Population Modelling

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Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed American Eel (*Anguilla rostrata*) as Threatened in Canada, due to dramatic declines over a significant portion of its distribution (COSEWIC 2012). In support of a recovery potential assessment (RPA) for American Eel, we present population modelling of this panmictic species to assess population sensitivity to perturbation, and to compare possible dynamics of American Eel under various hypotheses regarding the distribution of eel larvae (e.g., maternal effects versus random distribution). Special attention is paid to transient dynamics (short term fluctuations in abundance as dynamics approach long term stability). The species' range was subdivided into RPA geographical zones. Population growth tended to be proportionally more sensitive to changes in natural mortality than in any other life history parameters, especially during early life stages (leptocephali, glass, elver), regardless of larval distribution assumptions. Sensitivity across zones was very dependent on larval distribution. Larval distribution also strongly influenced the type and duration of transient (short term, non-constant) dynamics observed in population projections. Scenarios with random distribution of larvae converged quickly to stable distributions, while strong maternal effects caused transient dynamics lasting 100s and 1,000s of years. These dynamics were often counterintuitive; apparent long-term growth and decline were both observed in populations with stationary vital rates (stable long-term abundance). Expected stable stage distributions also varied dramatically with larval distribution; if larvae were distributed by a "water attraction" hypothesis, 87% of spawners came from US zones, while eels were more distributed among zones with a "nearest neighbour" hypothesis. Stochastic simulations revealed large variation in possible trajectories and suggest that environmental variability may mask changes resulting from management or transient dynamics.

RÉSUMÉ

Évaluation du potentiel de rétablissement de l'anguille d'Amérique (*Anguilla rostrata*) pour l'est du Canada : modélisation de la population pour l'évaluation du potentiel de rétablissement

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a évalué l'anguille d'Amérique (*Anguilla rostrata*) comme étant une espèce menacée au Canada en raison d'importants déclins observés sur une grande partie de son aire de répartition (COSEPAC 2012). À l'appui d'une évaluation du potentiel de rétablissement (EPR) de l'anguille d'Amérique, nous présentons la modélisation de la population de cette espèce panmictique dans le but d'évaluer la sensibilité de sa population aux perturbations et de comparer les dynamiques possibles de l'anguille d'Amérique selon diverses hypothèses relatives à la répartition des larves (p. ex., effets maternels vs répartition aléatoire). Une attention particulière a été accordée aux dynamiques transitoires (fluctuations de l'abondance à court terme alors que les dynamiques s'approchent de la stabilité à long terme). L'aire de répartition de l'espèce a été divisée en zones géographiques aux fins de l'EPR. La croissance de la population avait tendance à être proportionnellement plus sensible aux changements de la mortalité naturelle que tous les autres paramètres du cycle biologique, et ce, surtout pendant les premiers stades biologiques (leptocéphales, civelles, anguillettes), peu importe les hypothèses concernant la répartition des larves. Dans toutes les zones, la sensibilité dépendait grandement de la répartition des larves. De plus, la répartition des larves avait une forte influence sur le type et la durée des dynamiques transitoires (à court terme, non constantes) observées dans les projections relative à la population. Les scénarios debutant avec une répartition aléatoire des larves ont rapidement convergé vers des répartitions stables, tandis qu'un effet maternel fort a causé des dynamiques transitoires durant des centaines et des milliers d'années. Ces dynamiques étaient souvent contre-intuitives; des croissances et des déclins apparents à long terme ont tous deux été observés pour les populations ayant des taux vitaux stables (abondance stable à long terme). Les répartitions stables par stade anticipées ont aussi connu des variations marquées par rapport à la répartition des larves; lorsque les larves étaient distribuées selon une hypothèse d'« attraction de l'eau », 87 % des reproducteurs provenaient des zones américaines, alors que selon l'hypothèse du « plus proche voisin » les anguilles étaient plutôt réparties parmi les zones. Des simulations stochastiques ont révélé une grande variation dans les trajectoires possibles et suggèrent qu'une variabilité environnementale pourrait camoufler les changements résultant de la gestion ou des dynamiques transitoires.

INTRODUCTION

The American Eel (*Anguilla rostrata*) is widely distributed in freshwater, estuaries, and coastal marine waters of the Western North Atlantic Ocean from northern South America to Greenland. American Eel spawn once, in the Sargasso Sea. Larvae (leptocephali) enter the Gulf Stream where they metamorphose into "glass eels" and are distributed the following year in coastal waters. As they move inshore, they develop into "elvers" and then "yellow eels". Eels reside in a variety of freshwater and marine habitats before maturing into "silver eels" and migrating back to the Sargasso Sea for spawning (Pratt et al. 2014).

The mechanism for dispersal of American Eel throughout its range is unknown. Genetic evidence suggests that American Eel consists of one panmictic population with complete mixing of spawning adults in the Sargasso Sea (Gagnaire et al. 2012; Côté et al. 2013). However, the life history of American Eel differs dramatically among regions where it is found, with region-specific growth patterns, lifespans, annual mortality, fecundity, and sex ratio (Vélez-Espino and Koops 2010; Cairns et al. 2014). One hypothesis to explain this diversity of phenotype involves random dispersal of offspring during the larval stage with spatially varying selection upon arrival (Gagnaire et al. 2012). Alternatively, migration of larvae to a particular latitude may be driven by factors such as the timing of larval metamorphosis, which may in turn be influenced by non-genetic contributions from females that modify the phenotypes of their offspring (maternal effects; Green 2008). For example, females from the northern portion of the range are larger and may therefore have larger eggs. These eggs may have more lipid reserves which may lead to delayed metamorphosis, bringing the larvae further north and closer to the latitude of their female parent.

There is scant evidence to support any proposed larval distribution hypotheses over others, and hypotheses regarding causal mechanisms tend to be speculative. We therefore have developed a model that represents the entire population of American Eel, and can be easily modified to represent several hypothesized larval distribution scenarios. We present results that explore the extremes of these scenarios with the goal of describing the range of possible population dynamics and their sensitivity to larval distribution assumptions.

American Eel was designated as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2012) due to dramatic declines in abundance over significant portions of its distribution, especially Lake Ontario and the Upper St. Lawrence River. In accordance with the *Species at Risk Act* (SARA), which mandates the development of strategies for the protection and recovery of species that are at risk of extinction or extirpation from Canada, Fisheries and Oceans Canada (DFO) has developed the recovery potential assessment (RPA) (DFO 2007a; 2007b) as a means of providing information and scientific advice. There are three components to each RPA: an assessment of species status, the scope for recovery, and scenarios for mitigation and alternatives to activities. Here, we contribute to components two and three by

(i) identifying population sensitivity to perturbations,

(ii) employing population projections to explore and compare the dynamics of American Eel under various model assumptions, and

(iii) comparing the specific effects of anthropogenic mortality on the population across the range of assumptions.

This work is based on a demographic approach developed by Vélez-Espino and Koops (2007; 2009a; 2009b).

METHODS

Our analysis consisted of four parts:

(i) information on vital rates was compiled and used to build a population projection matrix, using uncertainty in life history to represent variation in the life cycle for stochastic simulations;

(ii) the matrix was used to determine the sensitivity of the population growth rate to changes in each vital rate following Caswell (2001);

(iii) the matrix was used to simulate population dynamics over time to compare the effects of various model and parameter assumptions on these dynamics; and

(iv) specific effects of anthropogenic mortality on the population were compared across the range of assumptions.

All analyses and simulations were conducted using the statistical program R (R Development Core Team 2012). All graphics were produced by the R package "ggplot2" (Wickham 2009)

THE MODEL

Using a matrix approach, the life cycle of American Eel was represented by a pre-breeding, age-structured projection matrix with annual projection intervals (Caswell 2001) (Figure 1, Figure 2). To explore the panmictic nature of American Eel, we chose to represent the entire species with one matrix. To represent the large variation in life history parameters, the population was divided into seven zones, as described in (Cairns et al. 2014), such that the life histories of eels within zones were relatively homogeneous (Table 1). Zones were represented by sub-matrices which were inter-connected only through reproduction (i.e., spawning eels from one zone may have offspring that migrate to other zones, but eels do not move between zones once they have arrived to continental areas). The life cycles of males and females also differ within each zone. We therefore employed a two sex model, so that each zone matrix tracked the abundance of males and females separately.

Each zone sub-matrix had classes for: migrating silver eels (male and female), larvae at sea (leptocephali), newly arrived elvers (considered to be age 0), and a class for males and females of each age. To reduce the number of dimensions for the model, each zone matrix was capped at the mean age of maturation (see Parameter Estimates). All older age classes were collapsed into a final stage class and assumed to share vital rates.

The model was designed such that leptocephali could be assumed either to be distributed among the zones without regard to parentage, distributed in proportion to how many silver females came from each respective zone, or by some combination of the two. The proportion of eels which is distributed to the maternal zone (d_m) can be set to 0 (no maternal effects on distribution), or 1 (population dynamics of all zones are completely independent of one another and depend entirely on their own female spawning stock), or any fraction in between. This parameter will henceforth be referred to as the "maternal effect" factor (d_m), and $1 - d_m$ as the non-maternal component of larval distribution. We compared four larval distribution hypotheses:

A. Full maternal effects (ME): Distribution of leptocephali is entirely driven by maternal effects; all leptocephali are distributed to their maternal zone ($d_m = 1$).

B. Full water attraction (WA): No maternal effects ($d_m = 0$); leptocephali are distributed to each zone ($d_{w,z}$), without regard to parentage, proportionally to the

area of North American watersheds that drain into the Atlantic Ocean from each zone ("water attraction" hypothesis; Table 1).

C. Hybrid maternal effects and water attraction (HWA): Strong maternal effects (95% of the leptocephali produced are distributed to the RPA zones according to the proportions of the parental females from each zone) and weak water attraction effect (5% of all leptocephali are distributed to RPA zones as in scenario B).

D. Hybrid maternal effects and nearest neighbour (HNN): Strong maternal effects as in scenario B for d_m, and weak straying to neighbouring zones (5% of leptocephali produced by females from each zone are distributed in equal proportions to immediate neighbouring zones (see Parameter Estimates; Table 1; Fig. 7).

Each zone matrix included a fecundity coefficient (F_z), the zone- and age-specific annual probability of transitioning from age class *j*-1 to class *j* ($G_{j,z}$), the zone- and age-specific probability of maturing to the silver eel class ($S_{j,z}$), and the probability of remaining in this final stage class ($P_{j,z}$). $P_{i,z}$ is the probability of surviving a year without maturing (1 - $G_{j,z}$), divided by the duration of the stage (i.e., the number of years remaining until the maximum lifespan for zone *z*).

Fecundity coefficients (F_z) for the HWA hypothesis represent the non-random contribution from females of offspring that will return to the same zone ($F_{z,z}$) plus the random contribution of offspring from all zones ($F_{z,zi}$):

(1) $$F_{z,z} + \sum F_{z,zi}$$

Each $F_{z,zi}$ or $F_{z,z}$ coefficient includes survival of adults during migration to the sea from zone *zi* ($M_{sea,zi}$; assumed to be the same as the survival of their age class), the expected number of offspring from a female from zone *zi* (η_{zi}), the survival of leptocephali traveling to zone *z* ($M_{lep,z}$), the proportion of leptocephali that will be distributed to zone *z* ($d_{w,z}$) and the maternal effect (d_m):

(2) $$F_{z,z} = \eta_z d_m \exp(-M_{sea,z} - M_{lep,z})$$

(3) $$F_{z,zi} = \eta_{zi} d_{w,z} (1 - d_m) \exp(-M_{sea,zi} - M_{lep,z})$$

Note that the distribution of leptocephali to each zone from females who came from that same zone includes the non-random component (proportional to the number of female spawners from that zone), plus the random component (proportional to $d_{w,z}$). To avoid including sex frequency dependence, it was assumed that reproductive output depends only on female abundance, and that there were always sufficient males for successful reproduction. This assumption was tested by including sex frequency dependence in an alternate model for comparison (see Methods: Population Projection).

For the HNN hypothesis, equations (1) and (2) were used. Equation (3) differed in that straying eels (eels not influenced by maternal effects) were distributed randomly and equally to neighbouring zones only (Table 1; Fig. 7). The contribution of straying leptocephali from zone *zi* to zone *z* was as per equation (4) when zone *zi* neighboured zone *z*, and zero otherwise. The number of neighbours to zone *zi* is represented by k_{zi}:

(4) $$F_{z,zi} = \frac{1}{k_{zi}} \eta_{zi} (1 - d_m) \exp(-M_{sea,zi} - M_{lep,z}) \, .$$

Coefficients for transitioning from age class *j-1* to age class *j* for zone *z* ($G_{j,z}$) combine several age-, zone- and sex- specific probabilities: not maturing, not dying of natural causes, and not dying of anthropogenic causes (fishing).

(5) $$G_{j,z} = (1 - pS_{j,z})\exp(-M_{j,z} - MF_z \cdot pF_{j,z})$$

Here, $pS_{j,z}$ is the probability of an eel from age class *j* in zone *z* maturing, $M_{j,z}$ is the instantaneous natural mortality of an eel in age class *j* from zone *z*, *MF* is the instantaneous mortality from fishing, and $pF_{j,z}$ is the probability of an eel from age class *j* being recruited to the fishing gear. When *j* = 1, equation (5) is multiplied by the proportion of females in zone *z* (r_z) for transition from elver to age 1 females, or the proportion males (1 - r_z) for transition from elver to age 1 males.

Similarly, coefficients for transitioning from class *j-1* to the silver class ($S_{j,z}$) combine probabilities of: maturing, not dying of natural causes, and not dying of anthropogenic causes (fishing or turbine).

(6) $$S_{j,z} = pS_{j,z}\exp(-M_{j,z} - MF_z \cdot pF_{silver,z} - MT_z)$$

Here, MT_z is instantaneous mortality from dam turbines.

Parameter Estimates

Definitions of parameter symbols are summarized in Table 2. Parameter values were compiled and summarized by zone. Additional details and discussion of sources and justifications can be found in Cairns et al. (2014) and are summarized below. Nearly all parameter values are based on the argument that demographic parameters vary according to geographic clines based on such predictors as latitude, distance from the spawning ground, and water temperature (Jessop 2010; Vélez-Espino and Koops 2010; Bevacqua et al. 2011). Mean values for distance from spawning grounds, latitude and mean water temperature by RPA zone are summarized in Table 3 (Cairns et al. 2014).

Growth

Mortality, probability of Silvering, and probability of recruitment to anthropogenic mortality were estimated separately for each age class. However, growth patterns of American Eel vary widely among and within zones, resulting in large variation in size at age. In addition, size has been found to be a much better predictor of maturation than age (Jessop 2010). We therefore used the expected length structure for each age to estimate mortality, probability of silvering, and probability of recruitment to anthropogenic mortality for each age class in each RPA zone.

Mean elver size was predicted to increase with latitude based on the data compiled by Cairns et al. (2013) (Table 4). Observed growth rates of male and female American Eel in each zone were used to develop predictive equations for mean growth rate (GR) based on either distance from the spawning ground (females) or latitude (males) for zones AN, AC, and AS. Where regressions were not significant, mean growth rate was used (males and females in zones SL, NG, SG and SF) (Table 5; Figure 3). Wherever mean growth rates were used, the standard deviation of the sample was used for variation. Wherever growth rates were predicted by regression, the standard deviation of the residuals was used (Table 6).

Growth of American Eel to maturation is thought to be relatively linear. However, maturation of American Eel depends on size, rather than age, which causes observed size at age to appear non-linear and asymptotic due to slower growing individuals taking longer to reach size at silvering (Cairns et al. 2014) (Figure 4). Therefore, the expected mean size at age (based on linear growth) differs from the observed mean size at age (of eels that have not yet matured). Expected length-at-age *a* (L_a) and variance at age is as follows:

(7) $$L_a = L_{elver} + GR \cdot a$$

(8) $$\mathrm{var}(L_a) = GR^2 \cdot var(a)$$

The means and variances of observed length-at-age for each zone were estimated by truncating the expected length-at-age distribution at mean silvering length (using the R package "truncdist", Novomestky and Nadarajah 2012). Mean silvering length for each zone was again based on clines: against distance for zones SL, NG and SG, and means for zones SF, AN, AC, and AS (Table 5) (Cairns et al. 2014). Length-at-age distributions were assumed to be lognormal as truncated expected lognormal distributions fit growth data from the Southern Gulf of St. Lawrence better than normal distributions (Figure 6.2.3 in Cairns et al. 2014).

The maximum age calculated from the cline-estimated growth rate for the SF zone was unrealistically high for females (75 years, see estimation method below). This was due to the relatively slow growth (19.1 mm/y) predicted by the growth rate clines derived from the mean distance from spawning ground of 3,550 km. The four growth rate observations for females from SF (Cairns et al. 2014) were all higher than predicted by the cline relationship (mean 26.1 mm/y). When this higher growth rate was used, the predicted maximum female age was 42 years, which is in agreement with observed maximum ages in the region. We therefore used the mean estimated growth rate for females in SF instead of the cline-predicted growth rate.

Probability of Maturation

Probability of maturing to the silver class was based on the expected length at age distributions; the probability of maturing was equal to the conditional probability of expected length being greater than silvering length, given that the expected length of the individual was not greater than silvering length the previous year. This was calculated by first determining the probability of being less than the silvering length at age *a*. The mean length at silvering varied by sex and region (Table 5). This probability (the proportion of immature eels of age *a*) was used to estimate the expected maximum length of these eels at age *a*+1. This length was used to truncate the distribution of length at age *a*+1, and to calculate the probability of maturing at age *a*+1 (Figure 5). Variability of these parameters for stochastic simulations was assumed to follow a beta distribution with shape parameters equal to the mean estimate (and 1 – the mean estimate) times 500. True variance in this parameter is unknown.

Maximum Age

Maximum age is not known for all zones. Therefore, maximum age was determined as the age at which the probability of the expected length (not observed length) being greater than the length at maturation equaled 95%, based on the mean and variance of growth rate for each zone. Maximum age increased with slower growth rate, larger variance, and larger length at maturation (Table 6).

Mean Age at Maturation

Mean silvering age was estimated by regression against distance to spawning ground, and was used to reduce the number of age classes in each zone; all age classes older than mean silvering age were collapsed into one stage class, and assumed to have the same vital rates. The geometric means of age-specific rates in the collapsed class were used.

Mortality

Natural Mortality

Cairns et al. (2014) compiled instantaneous natural mortality rates from the literature that were estimated using several different methods, all of which suffer from various limitations. For the sake of consistency across zones we estimated mortality using relationships developed for European Eel (Bevacqua et al. 2011). This relationship estimates instantaneous mortality (*M*) for male and female eels based on weight (*W*), temperature (C), and relative density, and can therefore give size-specific mortality (Figure 6). The study determined the coefficient b_{bev}, sex-

specific activation energy E, and density- and sex-specific coefficient a_{bev}, and used the Boltzmann constant k (for further details, see Cairns et al. 2014):

(9) $$M = a_{bev} \cdot \exp(-E/kC) \cdot W^{b_{bev}}$$

Length-weight regressions for each zone were used to convert mean length-at-age (mm) to mean weight at age (g) (Table 4). Elvers were often not included in the data used to determine these length weight regressions, and they did not predict elver weight well. A regression that used only elvers was used instead (Jessop 2003):

(10) $$W_{elver} = 0.00000043833 L_{elver}^{3.1084}.$$

Mortality of leptocephali and glass eels (i.e., from hatch to elver) is unknown. To estimate this rate, we assumed stable population growth rate in all zones ($\lambda_z = 1$), and determined the mortality at this stage that resulted in no change in population abundance, given all other parameter values and assuming independence among zones. Rates which give stable population abundance in the long term are referred to as "stationary rates". Alternative growth scenarios were also explored. For stochastic simulations, variations of mortality rates were derived using variations in length and weight at age, and assumed to be normally distributed.

Mean temperatures from Table 3 (converted to degrees Kelvin) were used in equation (9) with one exception: The mean temperature in AS zone was 20.8 °C, which was warmer than any of the sample sites used by Bevacqua et al. (2011) to determine the predictive mortality equation. As a consequence, elver mortality in AS was predicted to be so high that even 100% survival of leptocephali was insufficient to achieve a stable population growth. Since the temperature for AS was outside the range fitted for the Bevacqua formula, we used the warmest temperature within that range (18°C) to predict mortality in AS. This temperature was still within the estimated range of temperature for AS zone, and did not inhibit the calculation of stationary rates.

Anthropogenic Mortality

The probability of recruitment to fishing gear was estimated as the probability of eels of age *a* being larger than the size at recruitment to the gear (Figure 5). This probability was based on the length-at-age distributions truncated at silvering size. Silver eels were considered to be either 100% recruited to the gear or not at all, depending on the size at recruitment. The size at recruitment, or minimum fishing size, differs among zones. The Ontario American Eel fishery has been closed in SL zone since 2004 (COSEWIC 2012) but silver eels are still fished elsewhere in the SL zone; minimum fishing size was set at the female silvering size. Minimum sizes for NG, SG, and SF are 200 mm, 530 mm, and 350 mm, respectively (Chaput et al. 2014). Minimum fishing sizes for US zones (AN, AC, AS) was set at 152.4 mm (6 inches) (ASMFC 2012). Several scenarios for fishing mortality rates were explored.

Turbine mortality was assumed to apply only to migrating silver eels, and affected only eels from the SL zone for the purpose of this exercise (although the model is set up to accommodate turbine mortality variables in any zone). The SL zone consists of three water bodies or river segments: Lake Ontario and the St. Lawrence River (above the Moses-Saunders Dam; M-S), Lake St. Francis (between the M-S and the Beauharnois Dam), and the lower St. Lawrence River (below the Beauharnois Dam). Survival through the M-S dam is estimated to be 76.1% (Desrochers 1995). The Beauharnois dam has 3 routes that eels may take: 73.6% pass through Frances turbines (based on the distribution of flow) at 84.2% survival, 25.8% pass through Propeller turbines at 76.1% survival, and 0.6% pass by the turbines in spillage (Desrochers 1995), for an overall survival of 82.2% through the Beauharnois dam. Approximately 10% of

eels captured in the St. Lawrence River below both dams are from Lake Ontario (and have therefore passed through both dams; Tom Pratt, DFO, pers. Comm.). It is also known that approximately 5.4 times as many eels pass through the ladder at the Beauharnois dam into Lake St. Francis as do the ladder at M-S into Lake Ontario (Tom Pratt, DFO pers. comm.). Combining this information, we estimate that roughly 14% of eels in the SL zone come from Lake Ontario, 59% from Lake St. Francis, and 27% from the St. Lawrence below the dams, giving a net instantaneous turbine mortality of $MT = 0.17$.

Reproduction

Length-weight regressions from each zone, compiled by Cairns et al. (2014), were used to convert the estimated mean silver length to mean weight. From these, fecundities were estimated by weight-fecundity regression (Table 4, Table 6). For stochastic simulation, variance in fecundity was reported in some of these studies, and was otherwise estimated by extrapolating the coefficient of variance to the remaining zones (see Cairns et al. 2014).

Observed sex ratios were compiled in Cairns et al. (2014). Sex ratios in each zone were estimated as the mean of sex ratios estimated within that zone (Table 4).

Larval Distribution

Watershed areas and resulting proportions used for the water attraction hypothesis ($d_{w,z}$) are summarized in Table 1 (Cairns et al. 2014). Proportions were the same for WA and HWA hypotheses. Nearest neighbours for the HNN hypothesis were assumed to be as in Table 1 (Figure 7).

POPULATION SENSITIVITY

We are interested in the sensitivity of the estimated annual long-term population growth (λ) to perturbations in vital rate v. Annual population growth rate can be estimated as the largest (dominant) eigenvalue (λ_1) of an irreducible primitive projection matrix (Caswell 2001). Model sensitivity is quantified by elasticities, which are a measure of the sensitivity of population growth rate to perturbations in vital rate v, and are given by the scaled partial derivatives of λ with respect to the vital rate:

$$(11) \qquad \varepsilon_v = \frac{v}{\lambda}\sum_{i,j}\frac{\delta\lambda}{\delta a_{ij}}\frac{\delta a_{ij}}{\delta v},$$

where, a_{ij} are the matrix elements. Elasticities can be determined for the entire population or for any individual zone. That is, we can calculate the sensitivity of the whole population growth rate to changes in any parameter or, if we were to assume a zone to be independent of others, we could calculate the sensitivity of that zone's growth rate.

Elasticities can be used to predict the expected percent change in the long-term population growth rate ($\Delta\lambda$) as a result of a percent change in a vital rate (Δv):

$$(12) \qquad \Delta\lambda = \varepsilon_v \cdot \Delta v\ .$$

Since males were modeled such that reproduction depends only on females, the male life cycle is not a closed loop. The matrix is therefore reducible and imprimitive, which limits our ability to determine sensitivity analytically. Including a male contribution to reproduction requires frequency dependence, which requires that equilibrium structure be found in order to assess sensitivity analytically. Given that the type of sex frequency dependence experienced by American Eel is unknown, a female only (irreducible and primitive) matrix was constructed to conduct analytical sensitivity analyses. Sensitivity of population growth to male life history will depend on the type and magnitude of sex frequency dependence.

POPULATION PROJECTIONS

Deterministic Simulation

The population matrix was used to project abundances forward in one year time intervals. At each time step, abundances were summarized and recorded so that trajectories could be monitored for each life stage in each zone. Stages were summarized as: eels at sea; elvers in their first year (age-0); male, female and total yellow eels; and male, female, and total silver eels. Projections were modeled assuming four different sub-population trajectories:

i) all zones stable ($\lambda = 1$);

ii) all zones stable except population doubling every 10 years in SG zone ($\lambda_{SG} = 1.07$);

iii) all zones stable except population decline in SL (MF_{SL} increased); and

iv) all zone stable except population growth in SG and decline in SL as above.

For population growth, mortality in the first year at sea ($M_{lep,SL}$) was adjusted such that, were SG independent , the zone's abundance would double. For population decline in SL, fishing mortality (MF_{SL}) was increased. For each population growth scenario, the four different larval distribution assumptions described above were simulated.

Transient dynamics (temporary, non-stable dynamics that are observed as a population that is not in its stable stage distribution approaches this distribution) were explored. To do so, initial populations for each projection consisted of 50 billion leptocephali distributed according to the water attraction proportions (not a stable distribution). To explore expected dynamics following a change to a vital rate, initial populations were set to the stable stage distribution associated with the rates before the change. For example, the initial population was set to the stable stage distribution assuming decline in the SL (from increased fishing mortality). Projections were then run assuming stationary rates to explore the expected dynamics that might result from mitigation actions which decreased fishing mortality to the point of stability.

Stochastic Simulation

Stochastic simulation was used to explore the effects of uncertainty and environmental variation on population projections as follows:

i) 10,000 random values were drawn for each parameter using the means and variances and distributions described above, and used to form 10,000 random matrices, each representing a possible annual projection;

ii) population projections were performed by drawing one random matrix at each time step, with the initial population abundance set to be in the stable stage distribution;

iii) 100 separate projections were performed to create a distribution of possible outcomes.

The average stochastic growth rate was higher than that of the deterministic growth rate because

i) not all parameter distributions were normal, and

ii) growth from variable vital rates will emulate transient (not long term) growth.

For the purpose of observing variability in population trajectories, we increased leptocephali mortality in all zones for these simulations so that mean stochastic growth rate was roughly stable.

Sex Frequency Dependence

To test the model sensitivity to the assumption of sufficient males, we included sex frequency dependence in an alternative projection model. At each time step, the total number of spawning females for that year was scaled by the number of spawning males such that the effective number of spawning females (N_f') was the harmonic mean of the total number of males (N_m) and total number of females (N_f) (Caswell 2001):

$$N_f' = \frac{2N_m N_f}{N_m + N_f/h}. \quad (13)$$

Here, h is a factor allowing for polygyny, and represents the number of females one male can mate with. If $h = 1$, males and females mate 1 to 1. During simulation, if the number of males was insufficient to fertilize all eggs, this scalar reduced effective fecundity. If the number of males exceeded the required amount, the scalar was set to 1 (i.e., fecundity was not increased due to excessive males).

ALLOWABLE HARM

Allowable harm is defined as harm to the population that will not jeopardize population recovery or survival. If population growth rate is known, estimates of allowable harm are based on this rate and assume a minimum acceptable population growth rate of stability (λ=1). If population growth rate is known, maximum allowable harm (H) can be estimated analytically as:

$$H = \left(\frac{1}{\varepsilon_v}\right)\left(\frac{1-\lambda}{\lambda}\right) \quad (14)$$

where ε_v is the elasticity of vital rate v, and λ is population growth rate in the absence of additional harm.

Due to incomplete or inconsistent measures of abundance across zones, the current rate of population growth for American Eel is not known, and exact levels of allowable harm cannot be calculated for American Eel. For general guidance, we provide elasticity analysis; those parameters or life stages having the highest elasticity will be most susceptible to current or additional harm, and may be more receptive to recovery efforts.

For more specific guidance, we employ population projections to compare both long- and short-term effects of specific harm scenarios on each zone and on the entire population. For these scenarios, each zone was set at its stationary rates (adjusting M_{lep} such that $\lambda = 1$) assuming zero anthropogenic harm (no fishing or turbine mortality). Anthropogenic harm was then applied, and two outcomes were recorded:

i) the percent change in λ as a result of the harm (i.e., the expected annual decline in abundance over the long term, once the stable distribution is achieved); and

ii) the percent change in silver eel abundance after 50 years (approximately three generations).

These changes were recorded for each Canadian zone, for the Canadian population, and overall.

Five harm scenarios were considered. For all harm scenarios, anthropogenic harms in US zones (AN, AC, AS) were kept at 0, and anthropogenic harms in Canadian zones were set at approximations of current levels:

A. All harms:

i. silver eels are fished in SL ($MF_{SL} = 0.1$);

ii. yellow eels (and silver eels that have not migrated) are fished in NG, SG, and SF ($MF_{NG,SG,SF} = 0.1$);

iii. elvers are fished in SF ($M_{elv,SF} = M_{elv,SF} + 0.05$); and

iv. silver eels leaving Lake Ontario are affected by turbine mortality ($MT_{SL} = 0.17$).

B. No elver fishery: All harms in scenario A except elver fishery (iii).

C. No elver fishery, SL turbine mortality mitigated: silver and yellow eel fishery only from scenario A (i and ii).

D. No yellow or silver fishery: elver fishery in SF and turbine mortality in SL only from scenario A (iii and iv).

E. No fisheries: Turbine mortality from scenario A only (iv).

Each of these scenarios was also run assuming 25% and 50% reductions in the appropriate harms to simulate possible partial mitigation scenarios.

RESULTS

PARAMETER VALUES

Elver mortality, as estimated using the formula by Bevacqua et al. (2011), tended to decrease linearly with latitude due to the decrease in elver length and increase in temperature (c.f. equation 8). Conversely, the rates of leptocephali mortality (stationary rates) required to achieve stable populations in each zone tended to increase with latitude (Figure 8). This linear pattern is due in part to the requirements of stationary rates: if cumulative mortality from the elver stage is low, leptocephali mortality must be higher to compensate and achieve stability, and vice versa. Elver mortality and leptocephli mortality in particular were strongly (but not exactly) correlated ($r = -0.97$), suggesting that leptocephali mortality was largely determined by the estimates of elver mortality, but also influenced by the remaining parameters. There was a similar, less linear trend against distance to spawning ground. This result agrees with the expectation that leptocephali mortality should increase with distance from the spawning ground due to the longer migration duration.

POPULATION SENSITIVITY

Full Maternal Effects

The sensitivity of the model to changes in vital rates was similar in pattern across zones. Figure 9 shows elasticities for all parameters in each zone. Positive values indicate expected proportional increases in population growth rate if the vital rate is increased (equation (12)). Negative values indicate expected decreases in growth rate if the vital rate is increased. Elasticities were calculated assuming a fishing mortality of 0.1 in all zones, a turbine mortality of 0.17 in SL, and stationary rates in all zones (via adjusting leptocephali mortality). Figure 9 shows elasticity values for each zone assuming that all zones are independent of other zones ($d_m = 1$). That is, these are sensitivities of each zone's own growth rate to changes in its own parameters. Note that sensitivity of the overall population growth rate cannot be calculated via elasticity analysis because independent zones result in a reducible matrix (i.e., the eigenvalue of the matrix does not necessarily represent the long term growth of the whole population).

With the exception of AS zone, each zone's population growth rate is most sensitive to changes in leptocephali mortality, and sensitivity to mortality decreases with age. The rate of this

decrease differs among zones. For AS zone, elver mortality is proportionately most influential; this is likely due to the relatively large elver mortality in this zone.

Water Attraction

If any leptocephali were distributed to non-maternal zones via water attraction, sensitivity of the overall population growth rate to changes in any vital rate was a scalar of the sensitivities in Figure 9. Each zone's elasticities were scaled by a different, but constant, factor (Table 7). That factor was correlated with, but not directly determined by, the larval distribution parameter ($d_{w,z}$; $r = 0.93$). In other words, if non-maternal distribution occurs, the importance of one zone's contribution to the overall population growth rate is *approximately* scaled by the non-maternal distribution proportion ($d_{w,z}$), but cannot be exactly predicted by the factor. This is likely due to the differences in life histories among zones. For instance, elasticities for SL zone, which has exclusively large females with high fecundity, is scaled by a factor that is larger than its non-maternal larval distribution proportion, whereas AC and AS zones are scaled by factors that are smaller than their larval distribution proportions, indicating decreased importance compared to their distribution.

The properties of elasticities allow that they can be summed to show the sensitivity to changes in a group of rates (ex, mortality of all yellow age classes). Since threats or recovery efforts are more likely to affect entire stages rather than individual age classes, we present a summary of elasticities by life stage for leptocephali mortality, elver mortality, total yellow mortality, fishing mortality, turbine mortality, total probability of maturation across age classes, and larval distribution proportions (Figure 10 and Figure 11). Total susceptibility to the gear had the same elasticity as fishing mortality, and was not shown. Likewise, proportion of females had the same elasticity as fecundity. We also show these results organized in two different ways for comparison. The first shows elasticities separately for each zone to compare the importance of each variable within the zone (Figure 10). The second shows each variable separately to compare importance across zones (Figure 11).

Overall population growth was most sensitive to changes in leptocephali mortality in SL and NG ($\varepsilon < -0.2$). Within zones, for all zones except AS, population growth was more sensitive to proportional changes in leptocephali mortality than to elver mortality or all yellow eel mortality combined.

Among zones, the population growth rate tended to be most sensitive to changes in SL and/or NG. For elver and yellow mortality, population growth was most sensitive to changes in AS. The effects of fishing mortality were most significant in NG, least significant in SG and SF, and moderately significant in American zones. Differences in elasticities for fishing mortality among zones were in part due to different size restrictions; if a yellow eel fishery was included in SL, the elasticity was as large as that of NG. Conversely, population growth was least sensitive to changes in SG for all parameters. Elasticities for fishing mortality, recruitment to the gear, fecundity, percent female, maturation, and larval distribution proportions were all relatively lower (< 0.02). The elasticity for turbine mortality in SL was very small (~ -0.003).

Elasticities for a population with HWA distribution ($0 < d_m < 1$) did not differ from elasticities for WA distribution ($d_m = 0$) except for $\varepsilon(d_{w,z})$, which decreased to nearly zero as the strength of maternal effects was increased.

Hybrid Maternal / Nearest Neighbour

The pattern of elasticities differed across zones but not within zones when non-maternal distributions of larvae were assigned to neighbouring zones; the ranking of importance of the vital rates did not change, but the relative contribution of each zone to population growth was different. Elasticities for many rates (leptocephali mortality, maturity, fecundity) were highest in

NG, SG, and SF. Elasticities for elver mortality increased from Northern to Southern zones, and yellow mortality was relatively consistently important across zones. The elasticity for larval distribution proportions was zero in this case since this parameter was not used for nearest neighbour distribution.

Alternative Models

Declining Population

To test the influence of assuming stationary rates, elasticities were re-calculated in the following way: leptocephali mortality was calculated so that the population in its natural state (no fishing or turbine mortality) was stable, and fishing (0.1 for all zones) and turbine mortality (0.17 in SL) were added resulting in population decline ($\lambda = 0.961$). Elasticities were highly correlated with the stable scenario ($r = 0.92$) and were very similar in magnitude (some elasticities were slightly elevated, while others were slightly depressed). Notably, elasticities for SL were much stronger, especially for SL (< -0.3). In other words, when American Eel were in decline due to anthropogenic mortality, population growth was much more sensitive to changes in SL than when the population was stable, and the zone's relative importance increased.

Equal Larval Distribution

Elasticities for the water attraction hypothesis appeared to depend strongly on the larval distribution proportions. As a comparison, elasticities were calculated assuming $d_{w,z} = 1/7$ for all zones, ignoring for the moment any differences in amount of available habitat (Figure 13). Population growth was still dominated by leptocephali mortality in all zones but AS (note the different scales for each parameter). Fecundity, sex ratio, and larval distribution factors were equally important for all zones, but were unimportant relative to the mortality rate factors ($\varepsilon = 0.01$). The importance of fishing mortality increased in order of zone from AS to SL, but elasticities were also very small (> - 0.004).

POPULATION PROJECTIONS

Figure 14 through Figure 25 show the population of American Eel projected through time, with abundances tracked separately for each life stage (leptocephali, elvers, male and female yellows, and male and female silvers) as well as total abundance in all zones. Each figure compares different population growth rates (all zones $\lambda = 1$; all $\lambda = 1$ except one zone in decline; all $\lambda = 1$ except one zone growing; and all $\lambda = 1$ except one zone growing and one declining) and different assumptions regarding larval distribution. Except where otherwise stated, simulations assumed zero anthropogenic mortality. Each projection was initiated with a population of leptocephali only, distributed according to the larval distribution factors.

Recall that long-term model projections depend on the various assumptions of the model, which do not include responses to changing environmental conditions. For instance, if the simulation predicts extinction in the long term, this result does not account for possible life-history responses to low-density.

Projections of Stationary Vital Rates

Figure 14 to 16show projections over time of a population with stationary vital rates ($\lambda = 1$), for different larval distribution hypotheses.

Transient Dynamics

The eigenvalue of a population matrix represents the asymptotic population growth if present conditions are maintained indefinitely. Since it is unlikely that environmental conditions will

remain constant long enough for asymptotic properties to be expressed, it is useful to explore the transient dynamics (or short term dynamics) of the system as well (Caswell 2001).

Because population projections were started with a population of only leptocephali, the initial population was not in its stable stage distribution; all projections showed a degree of transient dynamics, which differed dramatically among zones. The rate of convergence to the stable stage distribution is governed by the magnitude of the second largest eigenvalue, relative to the dominant eigenvalue. This ratio is called the "damping ratio" (ρ), and can be used to estimate time to convergence. For example, the time required for the contribution of the second eigenvalue to decline to 5% of that of the dominant is $ln(20)/ln(\rho)$. If we define the time to convergence in this way, the time to convergence for independent zones ranged from approximately 30 years (for SL, NG, and SG) to 120 years (AS) (Figure 14), and correlated strongly with both distance to spawning ground (r = -0.90) and latitude (r = -0.97). Time to convergence was also related to the magnitude of oscillations as abundances approached the stable state.

The degree of transient dynamics was also affected a great deal by the larval distribution hypothesis assumed. With full water attraction (Figure 15), transient dynamics were brief compared to the assumption of full maternal effects (Figure 14), and time to convergence was only 16 years. On the other hand, when a small proportion (5%) of leptocephali were distributed via water attraction (HWA; Figure 16) or nearest neighbour straying (HNN; Figure 17) the time to convergence for the population was over 1,000 or 4,000 years, respectively. Transient dynamics were particularly apparent in those zones with longer independent times to convergence. For example, AS and AC zones were still increasing in abundance after 200 years, as was the total abundance. Here, transient dynamics resulted in long term population increase as abundances slowly approached the stable distribution and abundance. The hybrid maternal hypotheses converged differently; there was more oscillation with HNN than with HWA.

Declining Sub-populations

To explore the effects of a zone in decline on the whole species, projections were simulated using stationary rates for all zones except SL. Fishing mortality was set at 0.4 and turbine mortality at 0.17.

With full maternal effects, all zones stabilized except for SL, which declined at a rate of λ_{SL} = 0.972 (Figure 18). Note that the decline was exponential, but does not appear so with the logged scale. With full water attraction (d_m = 0), all zones converged to the same rate of long term decline (λ = 0.992) within approximately 17 years (Figure 19). While all zones eventually went extinct, the rate of decline in SL was slower than with full maternal effects due to a temporary rescue effect from other zones.

Both hybrid distributions resulted in eventual decline in all zones and extinction. However, stronger (but partial) maternal effects (i.e., higher d_m), resulted in slower overall rates of decline. For example, if d_m = 0.95 (5% straying), the overall rate of decline was only λ = 0.999 for HWA or HNN. Strong partial maternal effects also caused counterintuitive transient dynamics; SL declined immediately, but several other zones experienced growth for hundreds of years before decline was observed (HWA: Figure 20, Figure 21; HNN not shown). The time to convergence to the stable stage distribution (slow decline at equal rates in all zones) was nearly 2,000 years for HWA and longer for HNN.

Assuming that distribution of larvae does not change over time or with changing conditions, any declining zone acted as a sink provided maternal effects did not determine 100% of larval distribution. The overall rate of decline, however, depended on which zone was in decline and at

what rate. With HWA distribution, the effect of decline in any zone on the overall population growth rate was closely related to the larval distribution factors; the larger the proportion of larvae distributed to a zone, the faster a decline in that zone reduced the overall population.

Growing Sub-populations

To explore the effects of a growing zone on the whole species, projections were simulated using stationary rates for all zones except SG. Leptocephali mortality was reduced in SG such that the abundance of the independent zone was doubling every 10 years ($\lambda_{SG} = 1.07$).

With full maternal effects, only SG grew and the remaining zones approached stability (Figure 22). With any amount of random straying, SG acted as a source and all zones experienced growth in the long term. With full water attraction, all zones converged to a long term population growth rate of $\lambda = 1.003$ within a time to convergence of 16 years (Figure 23). This was slower than the growth that SG experienced with full maternal effects due to SG donating large amounts of its production to other zones. Conversely, if random straying was weak and maternal effects were strong (HWA; 5%; $d_m = 0.95$), the long term population growth rate was $\lambda = 1.066$ (Figure 24). This was nearly as fast as growth in SG with full maternal effects, but time to convergence was longer (50 years) than with full water attraction. Simulations with HNN distribution were similar, but with longer transient dynamics and increased oscillation in early years. Zones that neighboured the growing zone approached the long term growth rate more quickly than non-neighbouring zones.

Mixed Population Growth

Finally, projections were run with one growing and one declining population. Leptocephali mortality was reduced in SG such that, as above, abundance of the independent zone doubled every 10 years, and anthropogenic mortality was added in SL.

With full water attraction, overall population growth rate was dictated by the declining population. If only turbine mortality was present in SL ($MT = 0.17$), the decline in SL was almost exactly countered by the growth in SG, stabilizing the population ($\lambda = 1.0004$). If anthropogenic mortality was increased, SL again acted as a sink. For example, adding fishing mortality rates of 0.1 or 0.4 in addition to turbine mortality resulted in slow overall declines of $\lambda = 0.999$ or $\lambda = 0.995$ respectively. Conversely, with strong hybrid maternal effects and weak water attraction ($d_m = 0.95$), growth in SG was sufficient to rescue the declining SL population in the long term ($\lambda = 1.066$), with a time to convergence of 46 years (Figure 25). Again, HNN dynamics were similar to those with HWA.

Population Momentum

The section on transient dynamics above discussed changes in population structure of a population that is not in its stable stage distribution as it moves toward that state. Transient dynamics can also refer to changes in population structure that occur because a vital rate has changed, and the population distribution is shifting toward its new stable distribution. The difference between the population size before the change and after it has reached its new stable distribution is referred to as population momentum (Caswell 2001). This is of interest for conservation because, for instance, a declining population may continue to decline for a time before stabilizing, even if vital rates are equal to stationary rates.

Because the current stable distribution or current population growth rate for American Eel is unknown, we cannot predict population momentum resulting from management actions. Instead, we explored two possible scenarios. First, we assumed that all zones were at stationary rates except for SL, which had been growing (due to a higher leptocephali survival). We started the population projection at the appropriate stable stage distribution (i.e., the stable

distribution from all populations growing due to the increasing SL population). We then ran the projection supposing sufficient fishing and turbine mortality had been added to SL to return the zone to its stationary rates.

With full water attraction, population momentum was subtle (Figure 26); all zones continued to grow for a few years before stabilizing except for SL, which declined. Population momentum was more substantial with HNN (Figure 27); all zones except SL continued to grow for hundreds of years before stabilizing.

For the second scenario, the initial population distribution assumed all zones were at stationary rates except for SL, which had been in decline due to fishing pressure. Fishing pressure was removed for the projections so that all zones were at stationary rates. This resulted in an increase in yellow and silver eels in SL, and some (WA) or no (HNN) declines in other zones, but total abundance only fluctuated briefly before stabilizing at a similar abundance (not pictured).

Sex Frequency Dependence

When sex frequency dependence was included in population projections, population dynamics depended on the average number of females that each male could fertilize (h, equation (13)), and the stable state sex ratio of spawning silver eels (i.e., the ratio of total female silver eels to total male silver eels in a given year, once the population has stabilized). If h was larger than or equal to the stable sex ratio, dynamics were not affected by sex ratio (i.e., there were sufficient males for fertilization). If h was smaller than the stable sex ratio, the fecundity scalar fluctuated for a short time before stabilizing on a constant number less than 1 for the long term. This meant that the stable sex ratio was skewed too far toward females, and there were insufficient males for fertilization, resulting in constant population decline and extinction. It is important to note that this result depends entirely on the assumption of constant sex ratio at sexual assignment.

Stochastic Projections

Adding parameter variance resulted in large variation in population trajectories. Figure 28 shows the annual abundance of silver eels (by zone) over time that was realized in two out of the 100 trials conducted (with WA distribution). In one case, the population declined, while in the other it grew substantially. Both trajectories were simulated with vital rates drawn from the same distributions. Figure 29 shows the median and range of all 100 trials. Over time, the range of possible population trajectories increases dramatically. Note that

(i) mean vital rates for each zone would result in population decline, and

(ii) the geometric mean of all eigenvalues in the trials was less than 1 (suggesting decline in the long term), but

(iii) the median population trajectory seems to be growing slightly.

The transient dynamics appear to promote growth in the short term, even though the average long term dynamic for each random matrix was that of decline.

STABLE STAGE DISTRIBUTIONS

Water Attraction

The stable stage distribution (ssd) was the same for all HWA distribution scenarios, regardless of the strength of maternal effects (i.e., for all $d_m < 1$).). However, the distributions across stages differed for each zone (Figure 30). For example, over 99% of the total eel population consisted of leptocephali headed toward AS zone, and yellow eels made up a larger proportion

of eels in NG zone than in other zones. In SL, AN, AC, and AS zones the stable proportion of leptocephali was larger than the proportion of yellow eels. In NG, SG, and SF the opposite was true (Figure 31).

Eels of all life stages were concentrated in AS zone, with the next largest proportion in AC (Figure 32), and some of the smallest proportions in NG and SL. In the stable state, 87% of spawners came from the three US zones (50% alone came from AS). While the larval distribution factors do not correlate with these zonal proportions ($r = 0.2$), they correlated strongly with the relative number of offspring from each zone (spawning females times fecundity, as a proportion; $r = 0.99$): 25% came from SL, and 22% from NG, while only 21% came from AS (Table 8).

Hybrid Maternal / Nearest neighbour

The stable distribution HNN was similar to HWA in how eels were distributed across life stage. However, the distribution across zones was different; yellow and silver eels were much less concentrated in AS and more evenly distributed in SF, AN, and AC, although proportions in SL, NG and SG were still lower (Figure 33, Table 8). Relative fecundity again differed from spawner proportions, but was this time concentrated in NG, SG, and SF. The stable abundance of silver eels was similar between HWA and HNN, but the total abundance (including leptocephali) was an order of magnitude higher for HWA.

The sex ratio at assignment did not differ from the stable sex ratio for HNN, and differed only slightly for HWA (Table 8). The overall stable sex ratio for both hybrid distribution scenarios was approximately 3:1 in favour of females.

Anthropogenic Mortality

Figure 30 to Figure 33 show stable distributions for pristine populations at their stationary rates (no anthropogenic harm). To test the sensitivity of the stable distribution to anthropogenic harm, fishing mortality was increased to 0.1 for all zones, and turbine mortality was added in SL. If leptocephali mortality was then adjusted to maintain stationary rates (stable abundance), the stable distribution across zones did not change significantly for either HWA or HNN distributions, although the proportion of silver eels compared to other life stages was reduced.

To test the sensitivity of stable distributions to the assumption of stationarity, leptocephali mortality was not adjusted before anthropogenic harm was applied (i.e., the model was stationary in the absence of anthropogenic harm, which caused decline when added). In this case, the distribution among zones changed dramatically for both hybrid water attraction (Figure 34) and hybrid nearest neighbour (Figure 35) if maternal effects were strong (Table 8). Most notably, the distribution of silver eels shifted from the southern zones to SL for both hybrid water attraction (66% in SL) and nearest neighbour (72%). In addition, over 80% of all offspring were produced by females from SL in both scenarios.

ALLOWABLE HARM

The effects of five harm scenarios on a population that was stable and unharmed were compared (Table 9). Declines were shown as percent change in silver eel abundance over 50 years in each Canadian zone, as well as in Canada overall, and percent change in the long-term population growth rate. Three larval distribution hypotheses were compared: full water attraction (WA), hybrid maternal effects / water attraction (HWA), and hybrid maternal effects / nearest neighbour (HNN). For each, harm was mitigated by 0%, 25%, or 50%. The following observations refer to the case of zero mitigation.

The decline in abundance caused by each scenario decreased in order from A to E. Decline in abundance and change in growth rate were similar for the two hybrid distribution scenarios; changes differed between HWA and HNN by < 7% in all zones, and for all harm scenarios. Declines in overall abundance were larger with hybrid scenarios than with full water attraction when yellow and silver eels were fished (scenarios A, B, C), but smaller otherwise (D, E). In other words, strong maternal effects reduced the ability of the three un-fished zones (in the US) to rescue the four fished zones (in Canada). On the other hand, when harm affected only SL (scenario D) or SL and SF (scenario E), strong maternal effects slowed the decline in abundance compared to full water attraction. The change to long-term population growth, however, was always largest with full water attraction.

Elver fisheries in SF (at the instantaneous mortality rate of 0.05) had very little effect on the population overall (comparing scenarios A and B: < 1% change in overall abundance, < 0.1% change in λ), and only slightly more on the individual zone (< 2% change in SF abundance), regardless of larval distribution.

Turbine mortality in SL had a larger effect (scenario E). With full water attraction, silver eels declined by 24% in SL, and 14% overall. With hybrid maternal effects, decline was greater in SL (39%) but less overall (11%, HWA; 4%, HNN).

Silver and yellow fisheries had a large effect (Scenario C), resulting in 67-77% decline in total silver abundance, depending on the larval distribution hypothesis. The change in long-term growth rate was larger for full water attraction (2%) than for hybrid scenarios with strong maternal effects (< 0.2%). Decline was greatest in NG (WA: 81%; HWA and HNN: 96%), likely due to the small minimum fishing size used in the projection. Fishing in the four Canadian zones caused decline in the three US zones (WA: 48 – 51%; HWA or HNN: 0 – 6%, not shown in table).

Note that percent change in abundance does not scale directly with percent change in population growth rate. This is due to transient dynamics; the former was determined by simulation while the latter was determined analytically from the projection matrix. Looking at scenario A, for example, the change in abundance over 50 years was larger for the hybrid hypotheses, while the change in population growth was smaller. This is because when there were strong maternal effects the "rescue" from other zones was slower, and the harm was more detrimental in the short term, than when there were no maternal effects. In the long term, however, the annual rate of decline was always slower when maternal effects were strong.

DISCUSSION

It is important to note that all results presented here are the product of model exploration, and were made without any calibration of the model to observed data. Results rest entirely on assumptions made about life history parameters and model structure, and often assume stability of the population abundance. They are intended to be used to compare possible expected dynamics given different hypotheses, and should not be used to provide quantitative predictions without first testing those assumptions.

Nevertheless, this model exploration revealed that while quantitative predictions are not necessarily robust to uncertainty, general patterns in elasticities, expected long term (stable) dynamics, and simulated trajectories were generally robust to parameter value uncertainty, but very sensitive to structural assumptions such as larval distribution. Parameter value uncertainty needs to be resolved to improve the predictive power of this model but, more importantly, a greater understanding of larval distribution is required to predict future dynamics of American Eel, and to assess the potential for dynamics in one zone to affect the entire population.

PARAMETER UNCERTAINTY

Mortality

Leptocephali mortality estimates were determined by assuming equilibrium (stable abundance). As such, they depended entirely on other parameter choices for lifespan, fecundity and mortality. They were especially influenced by elver mortality, which in turn relied on the appropriateness of extrapolating the formula by Bevaqua et al. (2011) to small body size.

Due to the heavy reliance on the mortality allometry, our mortality estimates are somewhat uncertain. However, the allometry provides relative estimates between zones that are likely sufficiently robust for the purpose of comparing dynamics across hypotheses. The fact that stationary values for leptocephali mortality were achievable is encouraging; if a mortality of 0 or 100% were required in any zone, it would have been cause to revisit some or all of the parameters for that zone.

We considered scaling leptocephali mortalities by distance from spawning ground to account for differing times spent migrating to the coast. However, any scaling method we considered was entirely invented and arbitrary. In addition, the observed relationship between distance from the spawning ground, latitude, and mortality (Figure 8) indicated that an additional scaling might be redundant.

Individual Growth

Many parameter values relied on assumptions regarding growth of individuals. Mortality was based on size at age, and maximum age, probability of maturity, and recruitment to fishing gear were all highly influenced by the mean and variance of growth rates. Mean growth rates relied on clines, while the variance was largely influenced by the sample size of observed growth rates used for predictive regressions. As was seen in SF zone, a small change in growth rate (from 19 to 26 mm/year) resulted in a change in maximum age from 75 to 42 years. All other predicted maximum ages seemed reasonable, given mean ages at silvering, but the probability of silvering is unknown for most zones and cannot be compared. It should also be noted that the samples from which growth rate clines were estimated were largely biased toward fresh water, and may therefore underestimate growth rates in some zones. It should also be noted that all of the observations of size and growth rates from NG zone were from the Newfoundland part of Northern Gulf and Newfoundland.

Sex Ratio

The sex ratios used to assign sex were based on observed ratios of silver eels. Due to the different life spans of males and females within a zone, this is potentially not ideal, as the observed ratio may differ from the assignment ratio. In this case, however, there was not a dramatic difference between the assignment ratio and the stable state ratio (Table 8). The largest differences were in AC and AS, which had 12% fewer and 14% more females in the stable state, respectively.

Current Abundance

Because relative abundances across zones were unknown, initial abundances for each zone were chosen arbitrarily and likely do not reflect the true distribution of abundances of American Eel. Likewise, the age distributions of eels were not known for most zones. Knowledge of current abundances and distributions would allow for more relevant quantitative simulation of expected population trajectories.

MODEL RESULTS

Elasticities

The overall population growth rate was most sensitive to proportional changes in natural mortality of leptocephali in all Canadian zones. Uncertainty in this parameter (compared to other parameters) is most likely to affect the predictive power of this model, and should be resolved. However, we are unlikely to be able to affect this rate through management; the most relevant parameter for management is likely fishing mortality. Of all Canadian zones, population growth was most sensitive to fishing in NG zone, likely due to the smaller fishing size limit.

It is important to note that the scope for change should be considered when using elasticities to guide management. For instance, a 10% change in adult mortality is much smaller in absolute value than a 10% change in elver mortality, and may therefore be more feasible. In addition, if any rate is already close to the maximum natural (unharmed) rate, improvement in that rate may not be biologically possible.

Relative Contribution of Zones

The overall population growth rate of American Eel was most sensitive to proportional changes in mortality of leptocephali heading to SL or NG zones, followed by mortality of elvers in AS (Figure 10). When parameters were compared across zones, values for SL, NG and/or AS were always most influential under the water attraction (or hybrid maternal effects / water attraction) hypothesis, while NG, SG, and SF tended to drive dynamics under the hybrid maternal effects / nearest neighbour hypothesis. Water attraction had a large impact on the influence of each zone, as indicated by the strong correlation between distribution and elasticities of a zone. When larvae were distributed equally among zones, the pattern of elasticities among zones differed greatly, although leptocephali mortality was still the most important rate, as was elver mortality in AS.

Under the water attraction hypothesis, females from SL, NG and AS produced the largest proportions of offspring in the stable state (21 – 26%). These values were also highly correlated with the distribution factors ($r = 0.99$). Any predictions about population growth based on this model will be highly influenced by the distribution factors, which are also among the most uncertain estimates in this model and deserve a great deal of further attention. Predictions will also be strongly influenced by the distribution hypothesis; under hybrid maternal effects / nearest neighbour distribution, offspring production was more evenly spread, with the largest proportions from NG, SG and SF (18 -19% each). Finally the relative contributions from each zone changed dramatically if zones were in decline (rather than stable); in this case, the majority of offspring were produced by females from SL in the stable state for both water attraction and nearest neighbour hypotheses (84 - 95%).

Sinks and Sources

Under the given model assumptions of no limits on carrying capacity, no density-dependence, and no environmental variation, it was an expected result that, given some level of straying, decline in one zone lead to declines in all others and eventual extinction (assuming stability of all other zones). Likewise, growth in one zone lead to growth in all others. If one zone was in decline and one growing, one of the zones would eventually dominate the long term dynamics. We did not anticipate, however, the effect of straying rate on the rate of growth or decline.

Under full water attraction, the observed rate of decline in a declining zone was slower than expected due to "donated" leptocephali from other zones. Likewise, observed growth in a growing zone was suppressed due to donation of surplus leptocephali to other zones. With hybrid maternal effects with water attraction or nearest neighbour straying, however, immediate

decline in a declining zone was steep, but long term decline was slowed nearly to stability by donated eels. Conversely, long term growth with low straying or weak water attraction approached the expected growth rate for the independent zone. In other words, weak water attraction or a low rate of straying was more beneficial in the long term than full water attraction for all zones if any zone was either growing (faster growth) or declining (better rescue, longer delay in population extinction). On the other hand, transient dynamics were such that full water attraction was more beneficial in the short term (faster growth, or faster immediate rescue of declining), but not in the long term (faster extinction).

In the case of one declining and one growing population, some maternal effects were also more beneficial than full water attraction. With full water attraction, decline dominated and lead to extinction. With strong maternal effects and weak straying, growth dominated.

Transient Dynamics and Population Momentum

The transient dynamics observed in population projections are an important result of this modelling exercise. Elasticity results are designed to comment on the long term growth of a population, and can predict population dynamics provided long term dynamics are achieved. Short term dynamics may run counter to long term expectations, and the likelihood of this is increased in a variable environment.

The transient dynamics observed in Figure 14 to Figure 26 were quite large, and mostly due to the initial population vector, which consisted only of leptocephali and was therefore not at all close to the stable state. This starting vector is certainly unrealistic, but was used to illustrate how much transient dynamics can affect population growth, and how those dynamics differed among zones and stages.

The duration of transient dynamics differed among zones, and was correlated with leptocephali mortality so that southern zones tended to experience longer instability than northern zones. The time to convergence was also affected by the strength of maternal effects, with full maternal effects resulting in the longest time to convergence, and a fully water attracted population converging relatively quickly.

The most important observation is that transient dynamics and population momentum can cause initial population growth in a population whose rates suggest stability or decline in the long term (or initial population decline when rates would suggest growth). This was demonstrated in several test scenarios. The first was when maternal effects were strong but incomplete, which seemed to result in extended transient dynamics lasting hundreds of years before stable states were reached. In these cases, both a population with stationary rates and one with decline in SL showed growth in many zones before stability or decline.

Some of these observed transient dynamics could likely be attributed to the choice of initial population. However, we also observed population momentum in unexpected directions when reasonable initial population vectors were chosen (Figure 26). The first scenario supposed previous population growth (caused by a high survival in one zone) followed by a reduction to stationary rates. The second assumed previous population decline (caused by overfishing in one zone) followed by a reduction of fishing pressure to stationary rates. The first scenario resulted in many years of continued growth before stability, while the second showed increases in the formerly overfished zone, and initial decline in other zones. It should be noted that population momentum would differ if a different vital rate had been adjusted, or if previous conditions had not yet reached stable state.

It is important to consider possible transient dynamics and population momentum both when forecasting future dynamics, and when trying to explain past observations. It is possible that observed decline or growth following a change in management or environment may be partly

explained by shifts from one stable state to the next. Certainly, knowledge of the true population distribution would reduce the amount of speculation required.

Population Abundances

The abundances simulated here are all entirely dependent upon initial population values, which were arbitrarily chosen. The actual numbers are thus not particularly meaningful. However, the stable stage distributions depended only on the parameter values (not initial abundances) and can be considered relatively robust, assuming no large changes in those parameter values. If the population trajectory and the abundance of one stage class were known (silver eels from the SL, for example), we could conceivably use the stable stage distribution to estimate abundances of other age classes. This could be done for each larval distribution hypothesis, allowing for comparison to known data. However, any such estimates would assume a stable state.

MODEL ASSUMPTIONS

Larval Distribution Hypotheses

Panmixia and the recruitment process to continental waters complicate the management of a species in a number of ways. If one zone is growing or declining, it may cause observed growth or decline in another zone that would otherwise be stationary. In addition, the true rate of growth or decline in a zone might be masked by donation of leptocephali to or from other zones. Certainly, the precautionary approach implies management of each zone as though it is independent. However, panmixia and larval redistribution make efforts to provide quantitative advice to one zone much more difficult in the absence of information from all zones.

A striking result of this modelling effort is the large variation in results for differing larval distribution hypotheses, even when the rate of non-maternal larval distribution was very low (i.e., when maternal effects were strong). Even very low levels of straying had very large consequences on population dynamics and the overall health of the population; with random distribution, a declining or growing zone can act as a sink or a source, affecting the entire population

Regardless of the biological plausibility of the full maternal effects hypothesis, it is logistically unrealistic. Some zone borders, especially along the Atlantic seaboard, were chosen for jurisdictional management purposes and divide what is more likely a gradient of parameter values into discrete segments. Even if such a gradient were modelled, leptocephali would have to distribute to their precise maternal location for zero straying between zones to occur. This scenario was included exclusively as a baseline reference to show how perturbations would affect an independent zone versus an alternate hypothesis where leptocephali are shared among zones.

The second scenario shows the extreme of completely random distribution, and employs one of many proposed mechanisms (water attraction) to guide that distribution. The hybrid scenarios were chosen to demonstrate the opposite extreme (strong maternal effects), as in A but with the more realistic assumption of straying. Hybrid maternal effects / water attraction was chosen to contrast with full water attraction, while hybrid maternal effects / nearest neighbour was chosen to demonstrate the variation observed between different random distribution hypotheses. Alternate scenarios can be easily explored within the framework of this model.

The values chosen for larval distribution to each zone under the water attraction hypothesis had a very large effect on the model results. Zones that received larger proportions of leptocephali (SL, NG and AS) tended to have more influence over long term population growth rate, and were responsible for most of the offspring produced each year, despite the skew toward

southern zones in total spawners. The method used to estimate the distribution proportions was based entirely on the hypothesis that larger amounts of water should accommodate larger amounts of fish, and requires further study and evidence.

Definition of Zones

The zones chosen for this model may not be the best possible representation of the American Eel population. The Carribean was excluded entirely, for instance, due to lack of data to parameterize such a zone. It is also possible that existing zones would be better represented as multiple separate zones. However, the overall patterns and observations about a panmictic species presented here will not change. If more quantitatively specific predictions are required, additional zones might be considered. This is only useful if the life history of the new zones is known, and differs from neighbouring zones.

Density Dependence

Real populations cannot grow indefinitely, as they do in these simulations. For instance, rescue of the declining SL zone by the growing SG zone assumed that SG could continue to grow sufficiently long for stability to be reached in SL. In reality, each zone will be subject to a carrying capacity, and eels may experience density dependence at any or all stages. While these simulations are instructive in that they show us how population dynamics would behave in an unrestricted scenario (at low population abundances, for instance), they should be interpreted with spatial and resource restrictions in mind.

Sex Ratio and Sex Frequency Dependence

Our model results assumed that there were sufficient males to fertilize all eggs. Given the sex ratios assumed for this model, and assuming sex ratios were fixed, and some level of random distribution occurred, the population required that males be able to fertilize an average of 3 females each (the stable state sex ratio). The stable state sex ratio depended on the assumed sex ratios in each zone, as well as other parameter values such as sex-specific mortality, and larval distribution. Any ratio lower than this value resulted in a constant rate of population decline, while any ratio higher had no impact on model results.

These straight forward results suggest that it is reasonable to exclude males from reproduction and assume a sufficient male population for the purpose of elasticity analysis and population projection. The actual number of females that any given male can fertilize is unknown, and should be confirmed to determine if insufficient male abundance is a factor in the decline of American Eel.

We caution that these conclusions regarding the impact of males on population dynamics rest not only on the sex ratios estimated, but on the assumption that these ratios are fixed. If there is a density dependent response in sex assignment, population decline due to insufficient or over abundant males may be corrected by changes in the sex assignment ratio. Such a compensation, in combination with frequency dependent reproduction, would result in an oscillating abundance.

Deterministic Versus Stochastic

Most of the results presented here were based on deterministic projections (i.e., no environmental variation). While this is certainly an unrealistic assumption, we feel there is value in exploring these dynamic patterns without introducing stochastic variation. However, the single stochastic projection presented here suggests that if vital rates vary annually, the observed dynamics can differ greatly from the expected values. Stochastic projections should be considered when using the model to provide specific quantitative advice.

ALLOWABLE HARM

Alternative Scenarios

This document presents expected population dynamics under a number of harm scenarios, compared across three different assumptions about model structure. The flexibility of this model allows for analysis of any number of additional scenarios. Model inputs that could be changed include: all life history parameter values for each zone including individual growth rate, the level of maternal effects, fishing or turbine mortality rates in each zone, minimum size for fishing or for turbine mortality in each zone, or the level of mitigation for these harms.

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TABLES

Table 1. Seven RPA zones of American Eel, with abbreviations, the relative sizes of each zone based on water attraction criteria, and the neighbouring zones, used in the population modelling.

Zone	Abbreviation	Water attraction proportions ($d_{w,z}$)	Neighbouring zones (n)
St. Lawrence Basin	SL	0.2653	NG, SG (2)
Northern Gulf of St. Lawrence and Newfoundland	NG	0.2340	SL, SG, SF (3)
Southern Gulf of St. Lawrence	SG	0.0274	SL, NG, SF (3)
Scotia-Fundy	SF	0.0627	NG, SG, AN (3)
Atlantic Seaboard North	AN	0.0988	SG, AC (2)
Atlantic Seaboard Central	AC	0.1217	AN, AS (2)
Atlantic Seaboard South	AS	0.1901	AC (1)

Table 2. Legend of parameter descriptions, symbols, references, and values used to model American Eel.

	Parameter	Description	Symbol	Values Used	Reference
Panmixia	Maternal effects	Proportion of larvae that migrate to the zone of their female parent	d_m	0, 0.95, 1	NA
	Larval distribution proportion	% of non-maternal distributed larvae that migrate to zone z	$d_{w,z}$	Table 1	(Cairns et al. 2014)
Reproduction	Percent female	By zone	r_z	Table 6	(Cairns et al. 2014)
	Fecundity	Mean eggs per female by zone	η_z	Table 6	(Cairns et al. 2014)
	Rate of Silvering	Annual probabilities by sex (*f,m*), age (*a*), and zone (*z*)	$pS_{fa,z}$; $pS_{ma,z}$	Figure 5	Methods
Mortality	Natural mortality	Instantaneous rate, by sex (*f,m*), age (*a*), and zone (*z*)	$M_{fa,z}$; $M_{ma,z}$	Figure 6	(Bevacqua et al. 2011; Cairns et al. 2014)
	Fishing mortality	Instantaneous rate by zone	MF_z	0, 0.1, 0.4	NA
	Rate of recruitment to the gear	Annual probabilities, by sex (*f,m*), age (*a*), and zone (*z*)	$pF_{fa,z}$; $pF_{ma,z}$	Figure 5	Methods
	Turbine mortality	Instantanous rate by zone	MT_z	0, 0.17 (SL only)	Methods
Matrix Elements	Fecundity coefficient	Effective fecundity (after mortality) from each zone to another	$F_{z,zi}$		Equations (2), (3)
	Transition coefficient	Probabilities of moving from one age class to the next	$G_{fa,z}$; $G_{ma,z}$		Equation (5)
	Silvering coefficient	Probabilities of maturing to the silver class	$S_{fa,z}$; $S_{ma,z}$		Equation (6)

Table 3. Latitude (mean, min. and max.), distance (km; mean, min. and max.) from the spawning ground, and mean annual water temperatures (°C; mean, min. and max.) by RPA zone (Cairns et al. 2014).

Zone	Latitude			Distance (km) from the spawning ground			Mean annual water temperature (°C)		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
SL	45.35	46.80	43.90	5,380	5,100	5,660	9.6	8.6	14.1
NG	49.05	46.60	51.50	4,410	3,860	4,960	4.90	1.5	9.99
SG	46.85	45.60	48.10	4,325	4,000	4,650	8.88	6.83	9.9
SF	45.20	43.40	47.00	3,550	3,100	4,000	7.0	7.0	7.0
AN	42.85	40.50	45.20	2,700	2,200	3,200	10.0	8.0	12.0
AC	38.55	36.60	40.50	2,050	1,900	2,200	13.5	12.0	15.0
AS	30.40	24.20	36.60	1,665	1,430	1,900	20.8	15.0	26.5

Table 4. Elver length (mm), large eel length (mm) to weight (g) regression coefficients, percent males, fecundity-weight regression coefficients, mean silver eel length (cm) and predicted fecundity by RPA zone (from Cairns et al. 2014).

Zone	Elver length (mm)	Length-weight regression coefficients		Percent males	Fecundity regression coefficients (weight)		Female silver eel length (cm)	Fecundity
		a	b		a	b		
SL	63.0	2.077 E-08	3.7008	0.0	390,841	0.483	90	13,155,712
NG	64.5	1.70373 E-06	3.0103	4.6	67,764	0.719	72	7,402,395
SG	63.1	5.1286 E-07	3.1970	1.5	147,231	0.592	70	6,550,316
SF	62.0	8.8716 E-07	3.1170	10.1	147,231	0.592	57	4,540,200
AN	60.4	9.8400 E-07	3.0900	44.7	14,608	0.915	57	2,916,282
AC	57.5	6.5000 E-07	3.1800	29.1	1,698	1.116	57	1,054,269
AS	52.0	1.92486 E-06	3.0067	13.0	1,698	1.116	57	1,054,269
Elvers (all zones)		4.3833 E-07	3.1084					

Table 5. Clinal associations (latitiude R-Lat; distance to spawning grounds R-DSG) of silver eel length (mm), silver eel age (years), and growth rate (mm per year), by RPA zone, based on clinal relationship regression coefficients or the mean value of observations in each RPA zone (as per Cairns et al. 2014).

Zone	Silver eel length (mm)				Silver eel age (years)				Growth rate (mm per year)			
	Regression coefficients		Length	Method	Regression coefficients		Age	Method	Regression coefficients		Growth rate	Method
	a	b			a	b			a	b		
Female												
SL	-117.541	0.1895	902	R-DSG	-7.71379	0.0053	20.9	R-DSG	na		49.3	Mean
NG	-117.541	0.1895	718	R-DSG	-7.71379	0.0053	15.7	R-DSG	na		49.3	Mean
SG	-117.541	0.1895	702	R-DSG	-7.71379	0.0053	15.3	R-DSG	na		49.3	Mean
SF	na		570	Mean	-4.68272	0.0070	20.3	R-DSG	118.893	-0.0281	19.3	R-DSG
AN	na		570	Mean	-4.68272	0.0070	14.3	R-DSG	118.893	-0.0281	43.1	R-DSG
AC	na		570	Mean	-4.68272	0.0070	9.7	R-DSG	118.893	-0.0281	61.4	R-DSG
AS	na		570	Mean	-4.68272	0.0070	7.0	R-DSG	118.893	-0.0281	72.2	R-DSG
Male												
SL	-155.3247	0.113	453	R-DSG	na		9.5	Mean	na		34.9	Mean
NG	-155.3247	0.113	343	R-DSG	na		9.5	Mean	na		34.9	Mean
SG	-155.3247	0.113	333	R-DSG	na		9.5	Mean	na		34.9	Mean
SF	na		349	Mean	-5.21668	0.0059	15.8	R-DSG	141.368	-2.6454	21.8	R-Lat
AN	na		349	Mean	-5.21668	0.0059	10.8	R-DSG	141.368	-2.6454	28.0	R-Lat
AC	na		349	Mean	-5.21668	0.0059	6.9	R-DSG	141.368	-2.6454	39.4	R-Lat
AS	na		349	Mean	-5.21668	0.0059	4.7	R-DSG	141.368	-2.6454	60.9	R-Lat

Table 6. Model parameters and values by RPA zone for proportion female (r_z), fecundity (η_z), elver length, growth rate, mean length and age at maturation (silver eel stage), and maximum age for males (m) and females (f). Where appropriate, mean and standard deviation (SD) are shown.

RPA Zone	Prop. Female	Fecundity		Elver length (mm)	Growth rate (mm/y)				Silvering length (mm)		Mean age at Silvering		Maximum age	
		mean	SD		f	SD	m	SD	f	m	f	m	f	m
SL	1	13.2 x10^6	3.2 E6	63	49.3	20.7	34.9	15.9	902	453	21	10	37	26
NG	0.954	7.4 x10^6	3.2 E6	64.5	49.3	20.7	34.9	15.9	718	343	16	10	29	19
SG	0.985	6.6 x10^6	1.5 E6	63.1	49.3	20.7	34.9	15.9	702	333	16	10	28	19
SF	0.899	4.5 x10^6	1.5 E6	62	19.3	10.9	21.8	5.1	570	349	21	16	42	20
AN	0.553	2.9 x10^6	8.6 E5	60.4	43.1	10.9	28	5.1	570	349	15	11	19	15
AC	0.709	1.1 x10^6	8.6 E5	57.5	61.4	10.9	34.4	5.1	570	349	10	7	12	11
AS	0.87	1.1 x10^6	8.6 E5	52	72.2	10.9	60.9	5.1	570	349	7	5	10	6

Table 7. Comparison of larval distribution proportions based on water attraction ($d_{w,z}$) and scaling factors for elasticities (by zone) under the assumption of full panmixia (dr = 0; no maternal effects).

Zone	d_z	Scaling factor
SL	0.2653	0.36
NG	0.2340	0.23
SG	0.0274	0.03
SF	0.0627	0.08
AN	0.0988	0.09
AC	0.1210	0.09
AS	0.1901	0.12

Table 8. Comparison of proportions female at sexual assignment with proportions female in the silver eel stage at the stable state distribution within each RPA zone, the proportions of silver eels (silver total) and of female silver eels (silver female) among zones in the stable state distribution, and proportions of total offspring (relative fecundity) among zones by silver females. Two larval distribution hypotheses are shown: hybrid maternal / water attraction and hybrid maternal / nearest neighbour, with maternal effect (d_m) set at 0.95. Values for a stable population with stationary rates and no anthropogenic mortality (Stn) are compared with values for a declining population (Decl.) subjected to fishing pressure ($MF_z = 0.1$) and turbine mortality ($MT_{SL} = 0.17$).

Hypothesis	RPA zone	Prop. female			Silver total		Silver female		Relative fecundity	
		at Asgmt.	Silver							
			Stn.	Decl.	Stn.	Decl.	Stn.	Decl.	Stn.	Decl.
Water Attraction	SL	1.00	1.00	1.00	0.04	0.66	0.05	0.73	0.26	0.95
	NG	0.95	0.95	0.92	0.08	0.01	0.07	0.01	0.22	0.01
	SG	0.98	0.99	0.98	0.01	0.01	0.01	0.01	0.03	0.01
	SF	0.84	0.90	0.74	0.03	0.02	0.03	0.02	0.06	0.01
	AN	0.58	0.55	0.52	0.11	0.02	0.08	0.01	0.10	0*
	AC	0.82	0.71	0.80	0.26	0.08	0.28	0.07	0.12	0.01
	AS	0.73	0.87	0.69	0.51	0.20	0.48	0.15	0.21	0.01
Nearest Neighbour	SL	1.00	1.00	1.00	0.02	0.71	0.03	0.72	0.12	0.84
	NG	0.95	0.95	0.92	0.06	0.03	0.07	0.03	0.18	0.02
	SG	0.98	0.98	0.98	0.07	0.24	0.08	0.24	0.19	0.14
	SF	0.84	0.84	0.75	0.11	0.02	0.12	0.01	0.19	0.01
	AN	0.58	0.58	0.52	0.17	0*	0.13	0*	0.12	0*
	AC	0.82	0.82	0.80	0.35	0*	0.37	0*	0.13	0*
	AS	0.73	0.73	0.69	0.22	0*	0.20	0*	0.07	0*

Table 9. Projected percent decline in silver eel abundance over 50 years when anthropogenic mortality (scenarios A – E; see text) was added to a stable population without anthropogenic mortality. Three larval distribution hypotheses are compared: full water attraction (WA), hybrid maternal effects / water attraction (HWA), and hybrid maternal effects / nearest neighbour (HNN). For each, anthropogenic mortality was mitigated by 0% (highlighted), 25%, or 50% from base values. Percent declines are shown for the Canadian zones (SL, NG, SG, SF), overall for the Canadian zone (CAN), and long term decline in population growth rate (λ) in the long term.

	WA			HWA			HNN		
	0	**25%**	**50%**	**0**	**25%**	**50%**	**0**	**25%**	**50%**
A) status quo: fisheries (silver, yellow, elver) + turbine mortality									
SL	61	52	40	55	46	34	57	47	35
NG	83	75	62	96	91	81	96	92	82
SG	67	58	45	70	60	46	71	61	47
SF	72	63	50	82	73	59	82	73	59
CAN	74	65	52	80	73	61	81	72	59
λ	2	2	1	<0.25	<0.25	<0.25	<0.1	<0.1	<0.1
B) fisheries (silver, yellow) + turbine mortality									
SL	61	52	40	55	46	34	57	47	35
NG	83	75	61	96	91	81	96	92	82
SG	67	58	45	70	60	46	71	61	47
SF	70	61	48	80	71	57	80	71	57
CAN	73	65	52	80	72	61	80	72	59
λ	2	2	1	<0.25	<0.25	<0.25	<0.1	<0.1	<0.1
C) fisheries (silver yellow)									
SL	47	40	31	27	21	15	30	24	17
NG	81	72	59	96	91	81	96	92	81
SG	62	53	41	69	59	46	71	61	47
SF	66	57	45	80	71	57	80	71	57
CAN	67	59	47	72	66	56	77	69	57
λ	2	1	1	<0.25	<0.25	<0.25	<0.1	<0.1	<0.1
D) fisheries (elver) + turbine mortality									
SL	24	19	13	39	31	22	38	30	22
NG	11	9	6	1	1	0	1	1	1
SG	12	9	6	1	1	0	1	1	1
SF	15	11	8	10	7	5	9	7	5
CAN	16	12	8	13	10	7	8	6	4
λ	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
E) turbine mortality only									
SL	24	19	13	39	31	22	38	30	22
NG	11	8	6	1	1	0	1	1	1
SG	11	9	6	1	1	0	1	1	1
SF	10	8	5	1	0	0	0	0	0
CAN	14	11	8	11	9	6	4	3	2
λ	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1

FIGURES

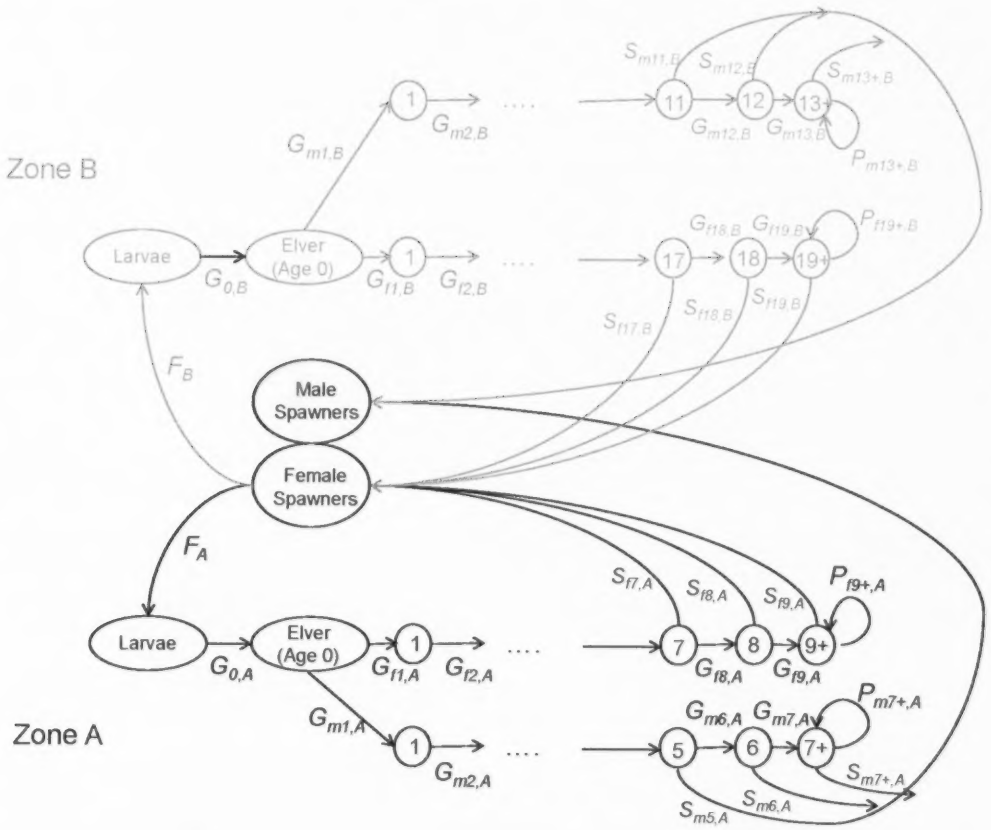

Figure 1. Life cycle diagram of an example American Eel population with two zones. F_z represents fecundity coefficients, $G_{fj,z}$ and $G_{mj,z}$ represent transition probabilities of age class j-1 to age class j in zone z for females and males, respectively, and $S_{fj,z}$ and $S_{mj,z}$ represent probabilities of maturing to the silver class and migrating to spawn. Maximum ages shown are arbitrary.

$$
\begin{array}{c|cccccccccccc|cc}
Sil_f^A & 0 & 0 & 0 & S_{f1,A} & \cdots & S_{f8,A} & S_{f9+,A} & 0 & 0 & \cdots & 0 & 0 & 0 & 0 \\
Lep^A & F_{A,A} & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & & 0 & 0 & F_{A,B} & 0 \\
Elv^A & 0 & G_{f0,A} & 0 & 0 & & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 \\
f_1^A & 0 & 0 & G_{f1,A} & 0 & & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 \\
\cdots & \cdots & & & & & & & & & & & & 0 & 0 \\
f_8^A & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 \\
f_9^A & 0 & 0 & 0 & 0 & & G_{f9,A} & P_{f9+,A} & 0 & 0 & & 0 & 0 & 0 & 0 \\
\hline
sil_m^A & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & S_{m1,A} & & S_{m7,A} & S_{m8,A} & 0 & 0 \\
m_1^A & 0 & 0 & G_{m1,A} & 0 & & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 \\
\cdots & \cdots & & & & & & & & & & & & 0 & 0 \\
m_6^A & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 \\
m_7^A & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & & G_{m7+,A} & P_{m7+,A} & 0 & 0 \\
\hline
Sil_f^B & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 \\
Lep^B & F_{B,A} & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & & 0 & 0 & F_{B,B} & 0
\end{array}
$$

Figure 2. Part of the population projection matrix corresponding to the example American Eel life cycle diagram in Figure 1. Each element represents contribution of the corresponding column stage to the row stage in the next annual census. Shown are the sub matrix for zone A including males and females (black in the life cycle diagram) and the Silver female and Leptocephali classes for zone B. Sil_f, Sil_m = Silver female and male classes, Lep = leptocephali class, Elv=elver class, f_j = female age j, m_j = male age j. $F_{z1,z2}$ = fecundity coefficient for zone z2 contributing to zone z1. $G_{fj,z}$, $G_{mj,z}$ = transition probabilities of age class j-1 to age class j in zone z for females and males, respectively, $S_{fj,z}$, $S_{mj,z}$ = probabilities of maturing to the silver class and migrating to spawn.

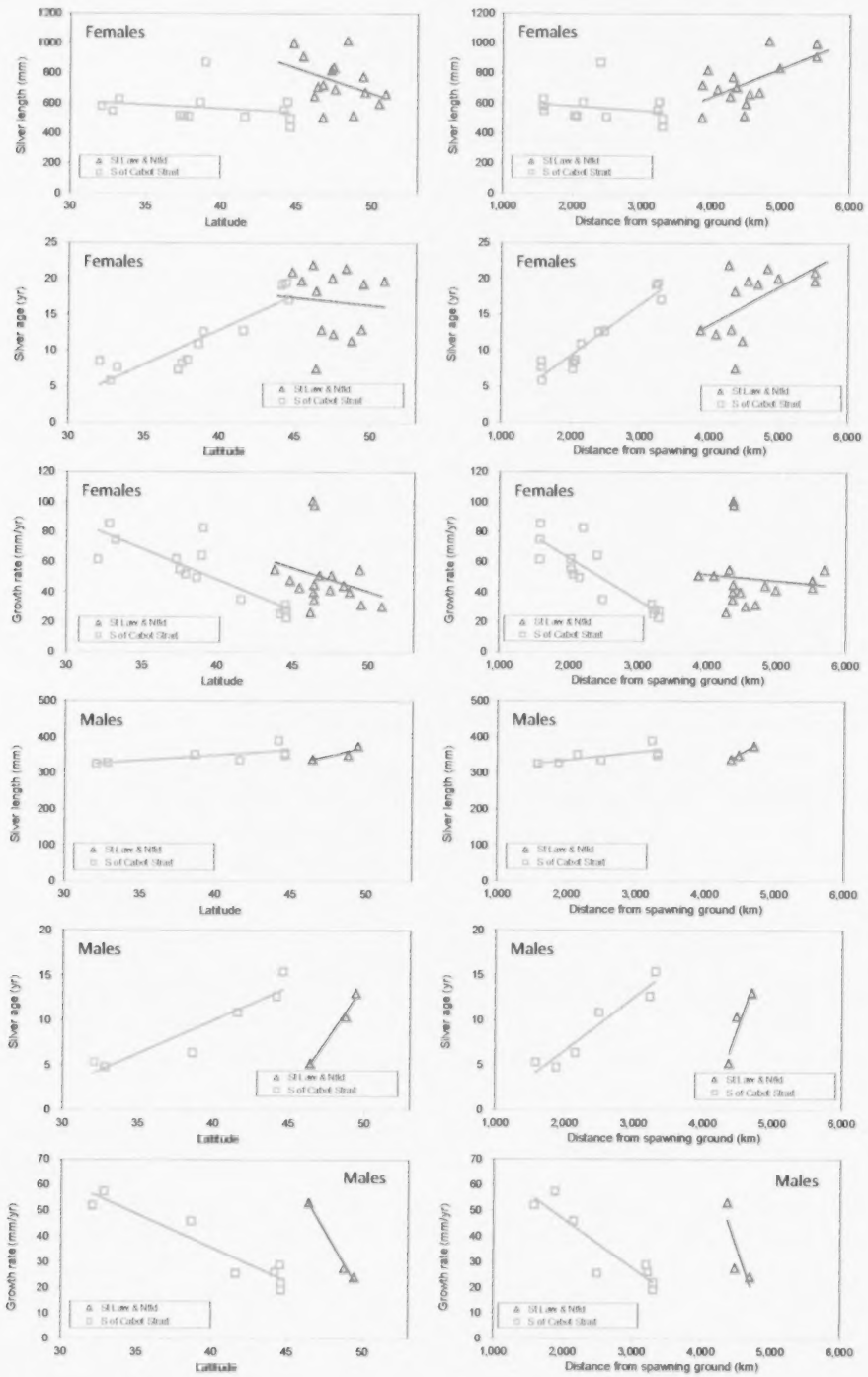

Figure 3. Relationships (Cairns et al. 2014) between American Eel silver length, silver age, and growth rate, with latitude and distance from the spawning ground, for females (top three rows) and males (bottom three rows). St Law & Nfld means the St. Lawrence Basin, the Northern Gulf of St. Lawrence and Newfoundland, and the Southern Gulf of St. Lawrence. S of Cabot Strait means Scotia-Fundy, Atlantic Seaboard-North, Atlantic Seaboard-Central, and Atlantic Seaboard-South.

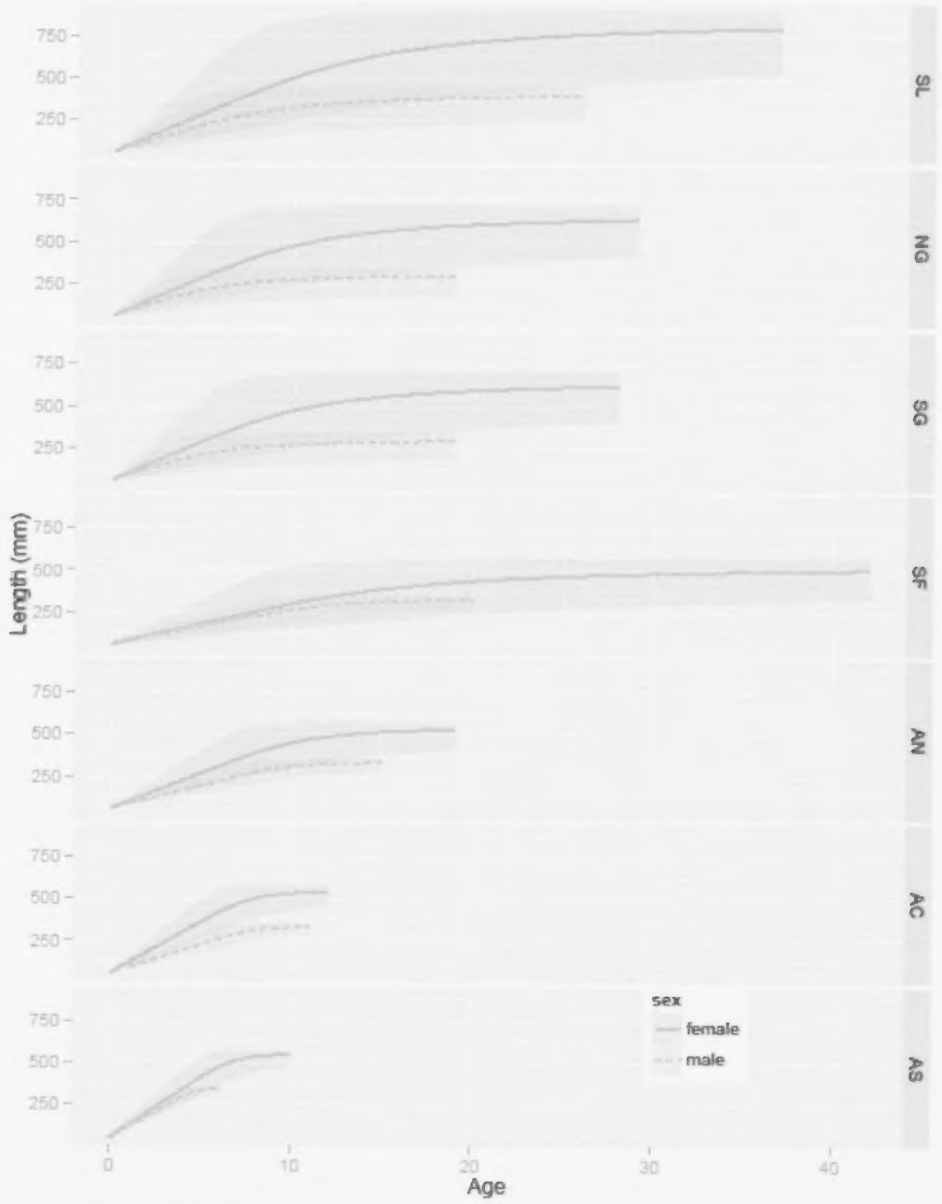

Figure 4. Estimated mean length-at-age (bold curves) with 95% confidence intervals (shading) for male and female American Eel by RPA zone. Mean and variance at age is based on expected growth and length distributions truncated at mean silvering length. Curves stop at estimated maximum ages (based on 95% probability of length being greater than silvering length).

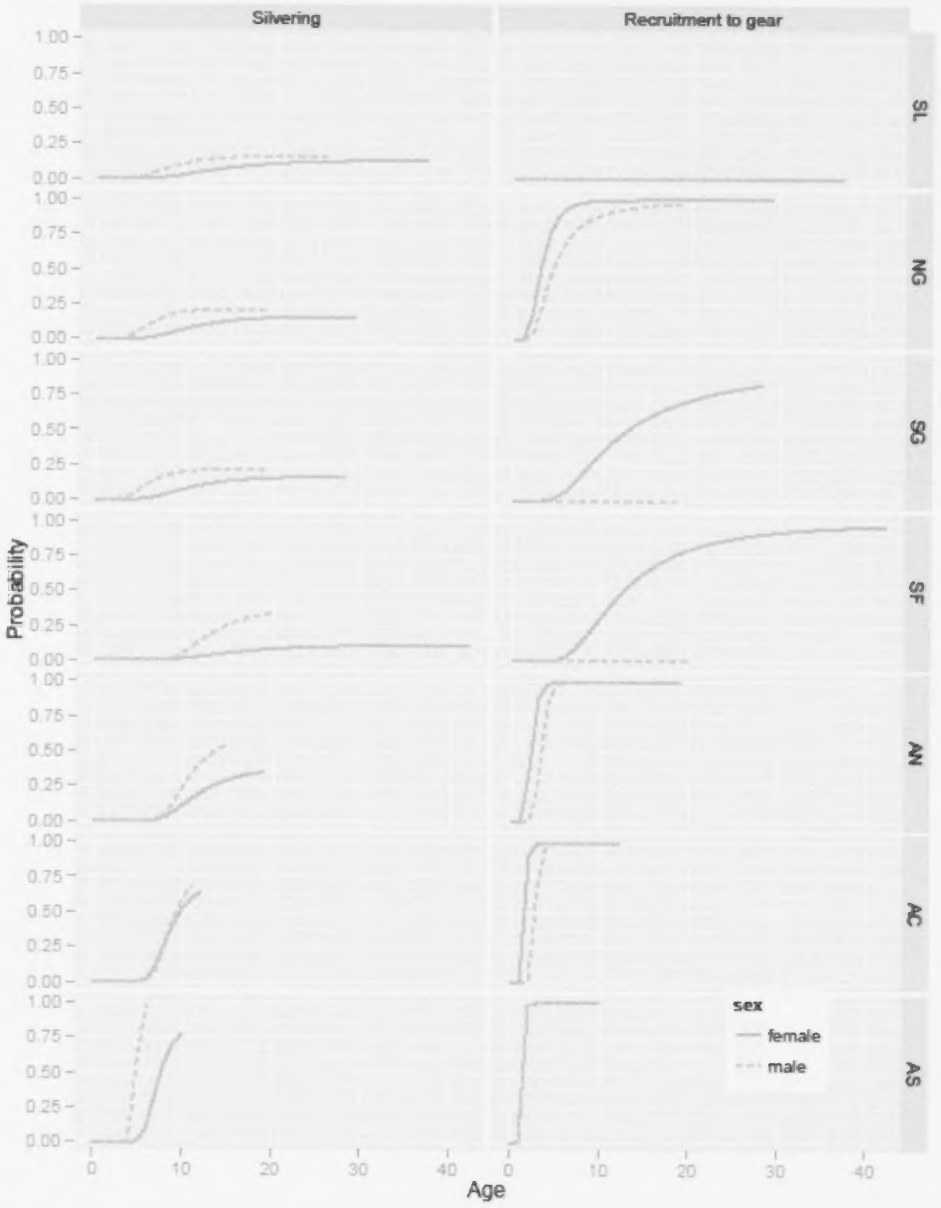

Figure 5. Probabilities of silvering and of being recruited to fishing gear by age, sex, and RPA zone, used in population modelling of American Eel. Zero values for SL reflect the closing of the yellow eel fishery in Lake Ontario. Migrating silver eels are still fished.

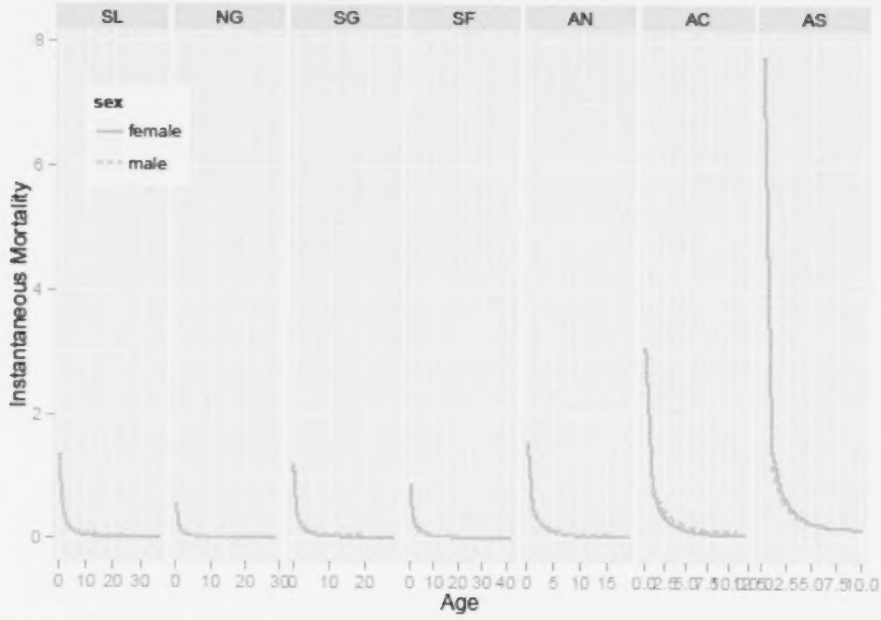

Figure 6. Age-specific instantaneous mortality used to model American Eel, by sex and RPA zone, from elver (age-0) to maximum age. Leptocephali mortalities are not shown as they are modelled rather than derived from the equations in Bevacqua et al. (2011).

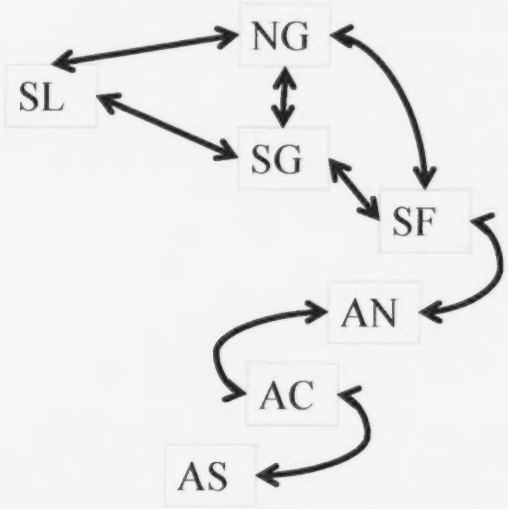

Figure 7. Diagram indicating (with arrows) nearest neighbour linkages among RPA zones used for the hybrid maternal / nearest neighbour larval distribution hypothesis. Zones lose leptocephali (at straying rate 1 – d_m) in equal parts to connected zones.

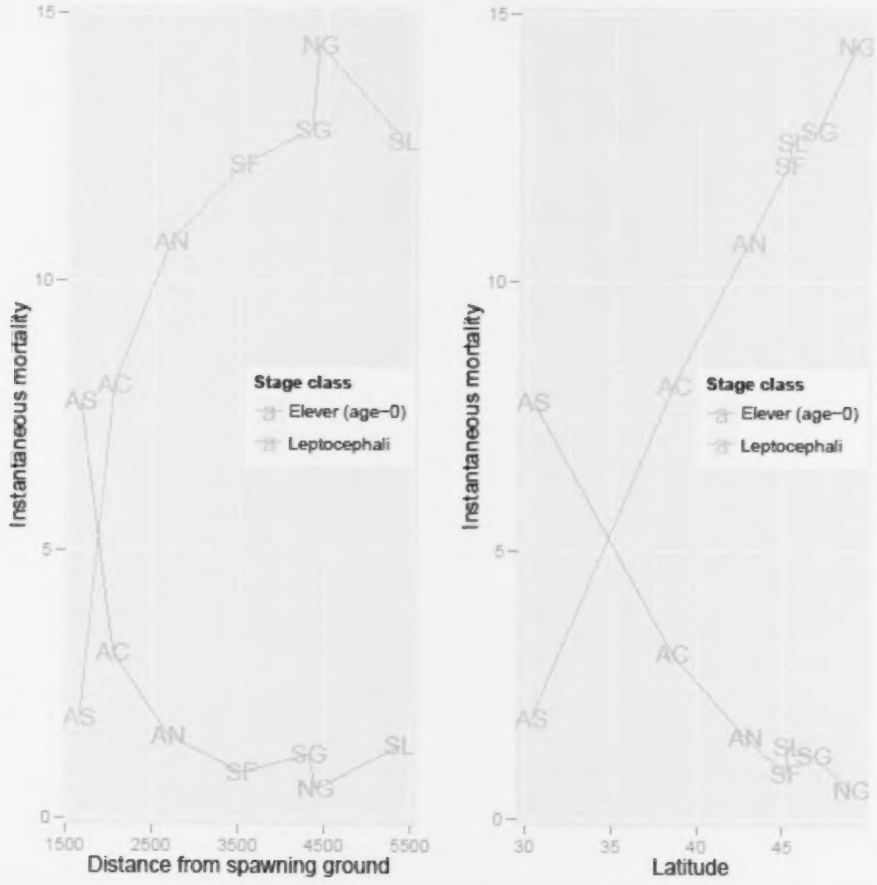

Figure 8. Elver and Leptocephali instantaneous mortality rates as a function of latitude, and distance to the Sargasso Sea, by RPA zone.

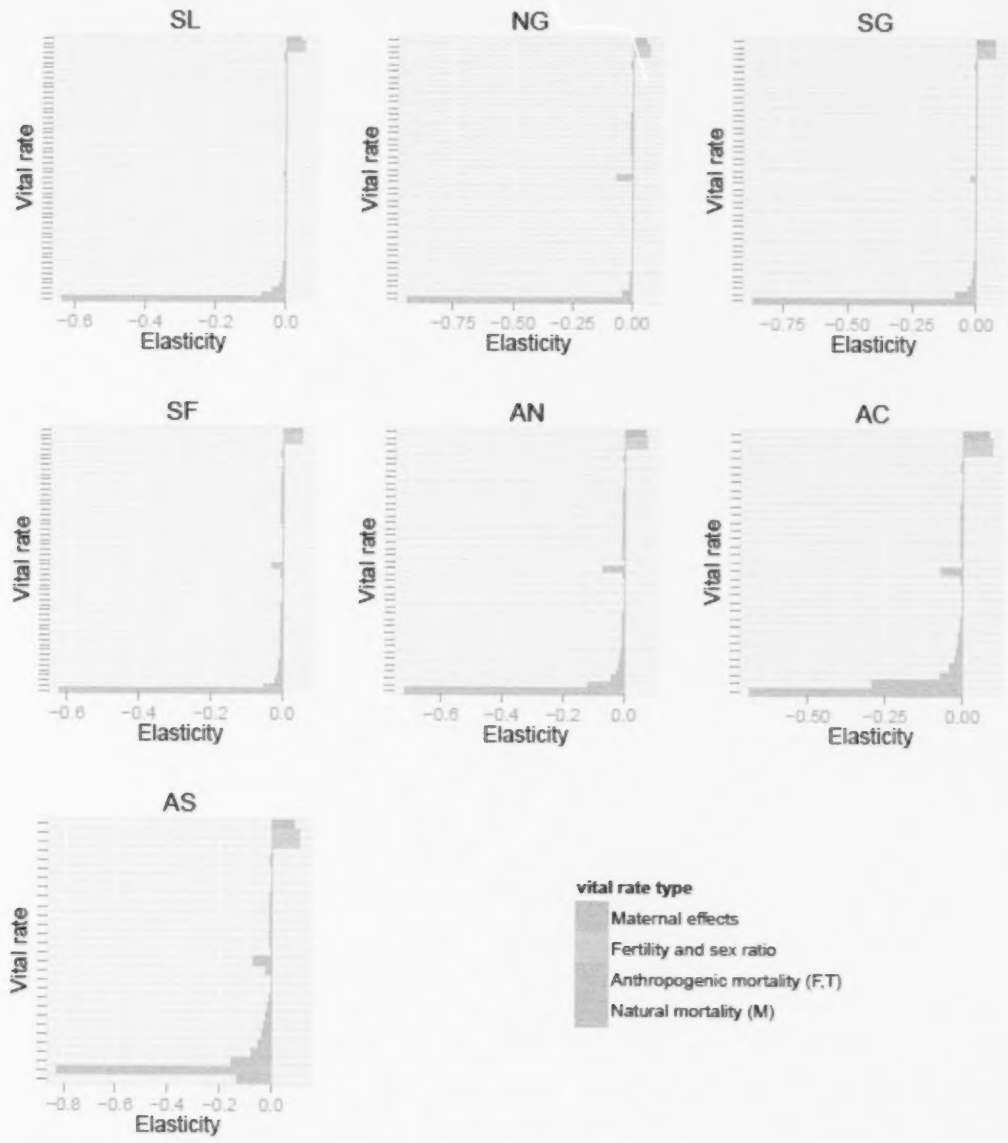

Figure 9. Elasticities for all parameters in each zone. Elasticities assume each zone is independent of others (fully maternal hypothesis, $d_m = 1$), stable ($\lambda = 1$). Parameters from top to bottom are: the maternal effects factor, fertility and sex ratio, anthropogenic mortality (turbine mortality, probability of recruitment to the gear, and fishing mortality – set to be 0.1 for all zones), and natural mortality by age class (bottom to top = youngest to oldest). Elasticities under a scenario with larval distribution among zones are scalars of these values.

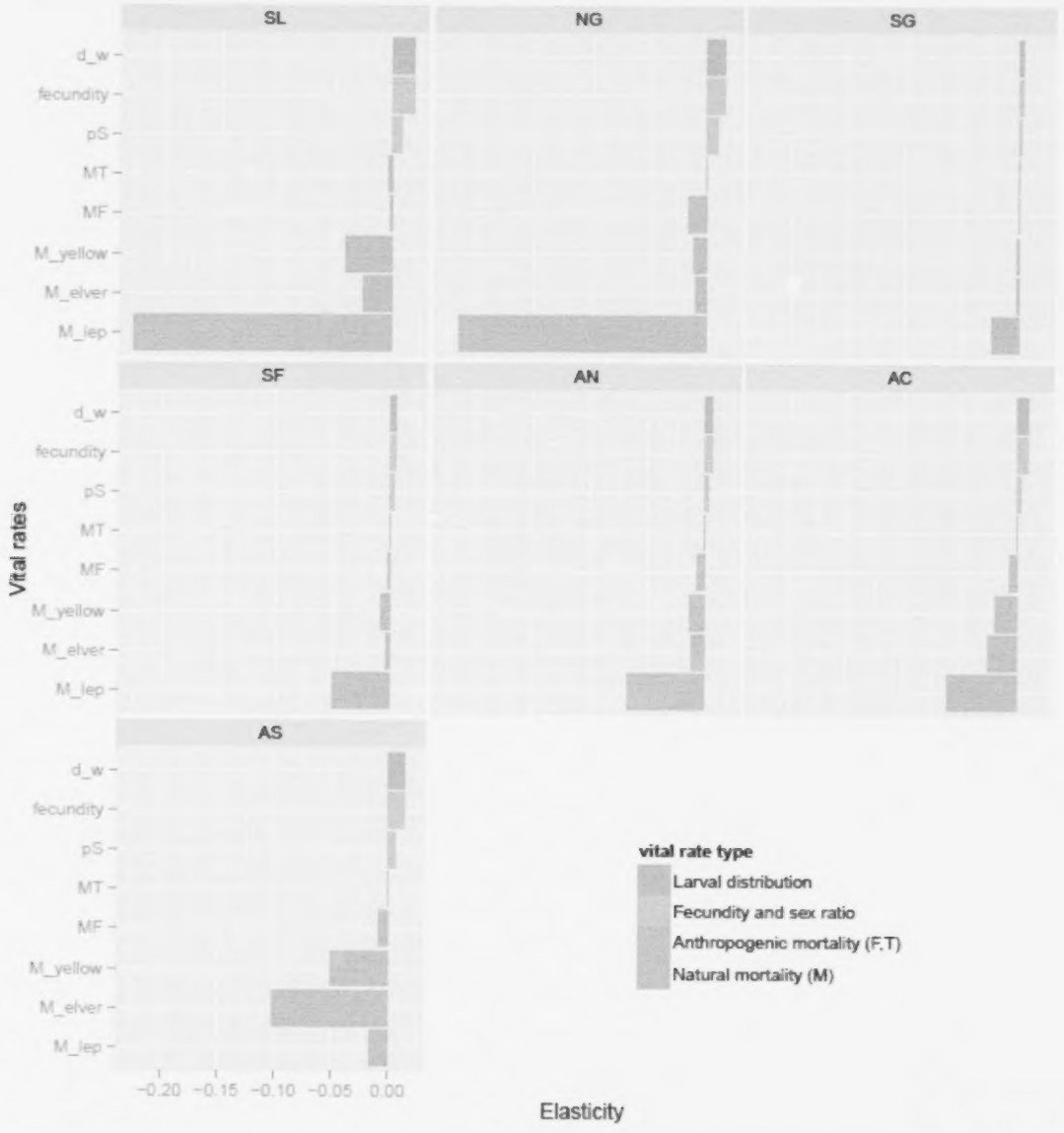

Figure 10. Summarized elasticities for each RPA zone, compared across vital rates. Parameter assumptions are: water attraction distribution (WA or HWA; $d_m = 0$), fishing mortality (MF) = 0.1 for all zones, turbine mortality (MT) for SL = 0.17, stable abundance ($\lambda = 1$). Elasticities from bottom to top are for: leptocephali mortality, elver mortality, total yellow mortality, fishing mortality (or probability of recruitment to the gear), turbine mortality, total probability of maturing, fecundity (or proportion females), and larval distribution proportion ($d_{w,z}$) for each zone.

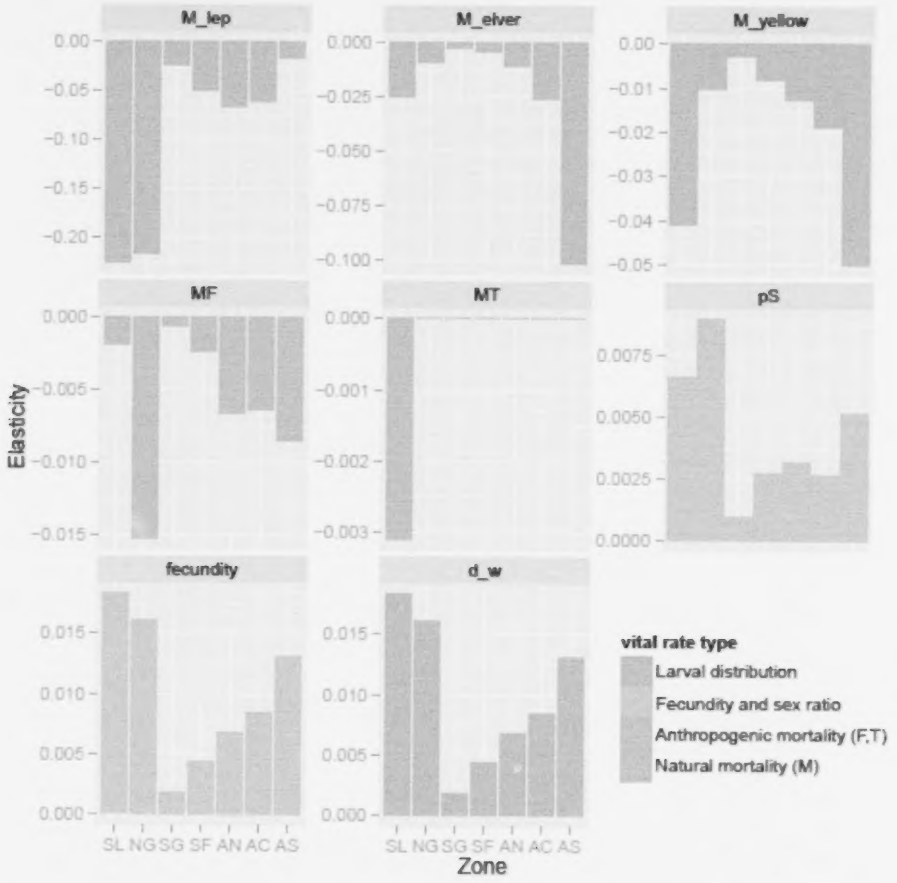

Figure 11. Summarized elasticities for each parameter, compared across RPA zones. Parameter assumptions are: water attraction distribution (WA or HWA; d_m), fishing mortality (MF) = 0.1 for all zones, turbine mortality (MT) for SL = 0.17, stable abundance ($\lambda = 1$). Elasticities from bottom to top are for: leptocephali mortality, elver mortality, total yellow mortality, fishing mortality (or probability of recruitment to the gear), turbine mortality, total probability of maturing, fecundity (or proportion females), and larval distribution proportion ($d_{w,z}$) for each zone.

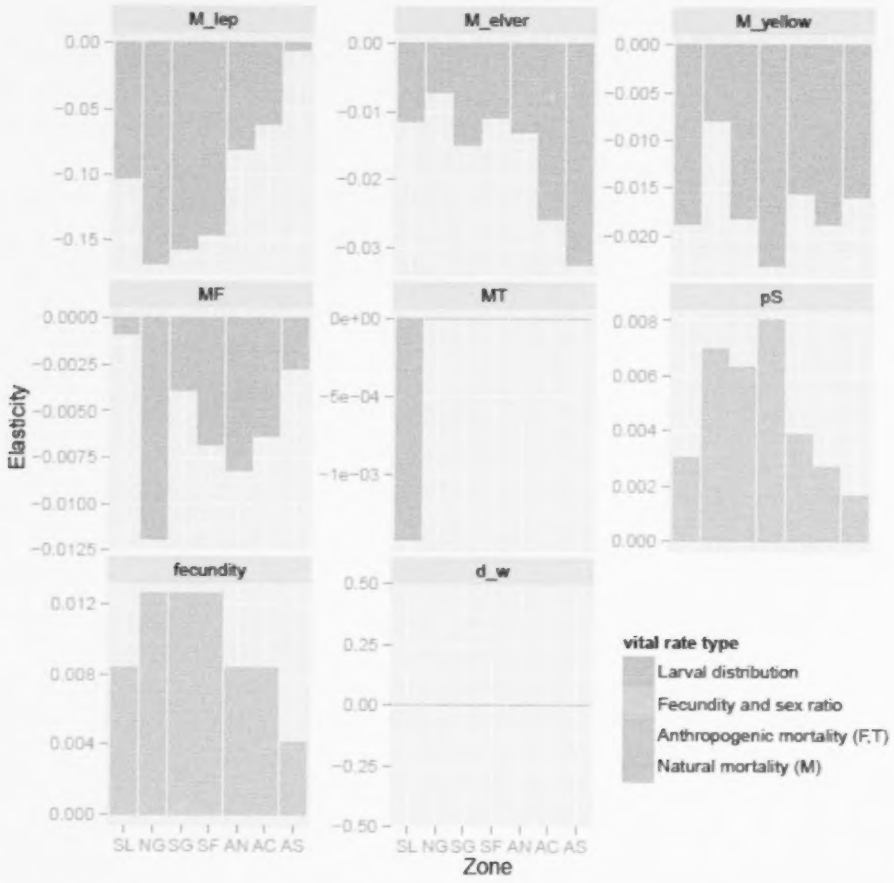

Figure 12. Summarized elasticities for each parameter, compared among RPA zones, with hybrid maternal / nearest neighbour distribution (HNN). Parameter assumptions are: Nearest neighbour straying at a rate of 5%. fishing mortality (MF) = 0.1 for all zones, turbine mortality (MT) for SL = 0.17, stable abundance (λ = 1). Elasticities from bottom to top are for: leptocephali mortality, elver mortality, total yellow mortality, fishing mortality (or probability of recruitment to the gear), turbine mortality, total probability of maturing, fecundity (or proportion females), and larval distribution proportion (d_w) for each zone.

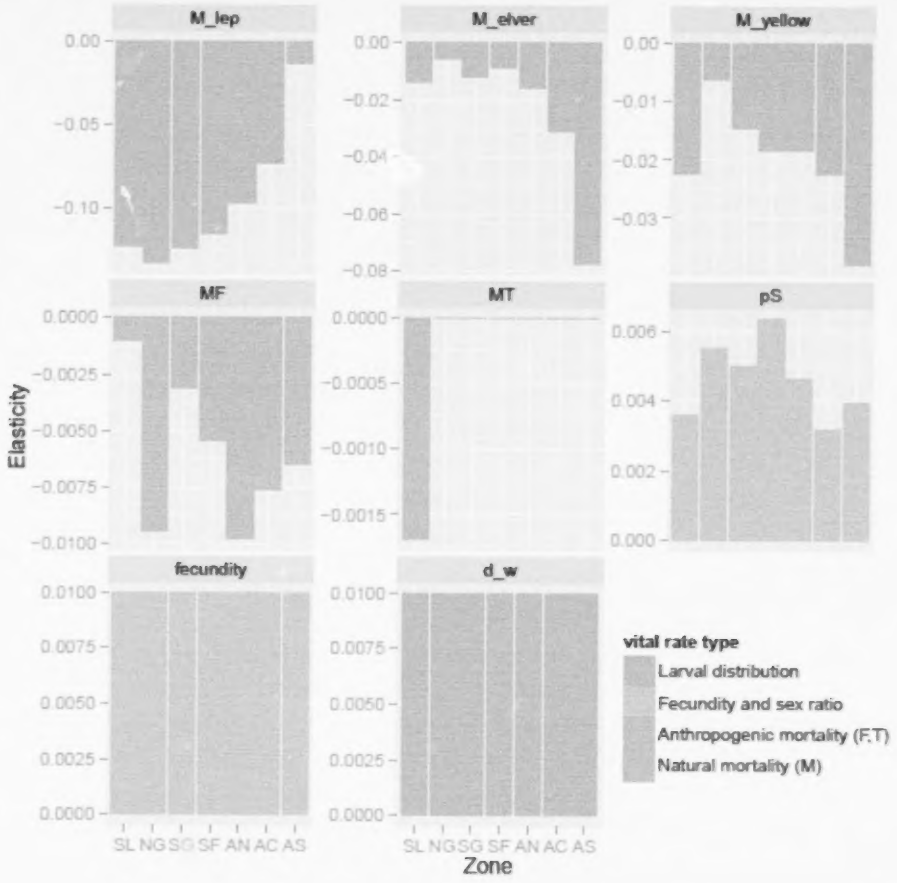

Figure 13. Summarized elasticities for each parameter, compared among RPA zones, supposing equal water attraction to all zones ($d_{w,z}$ = 1/7). Parameter assumptions are: fully random water attraction (d_m = 0), fishing mortality (MF) = 0.1 for all zones, turbine mortality (MT) for SL = 0.17, stable abundance (λ = 1). Elasticities from bottom to top are for: leptocephali mortality, elver mortality, total yellow mortality, fishing mortality (or probability of recruitment to the gear), turbine mortality, total probability of maturing, fecundity (or proportion females), and larval distribution proportion (d_w) for each zone.

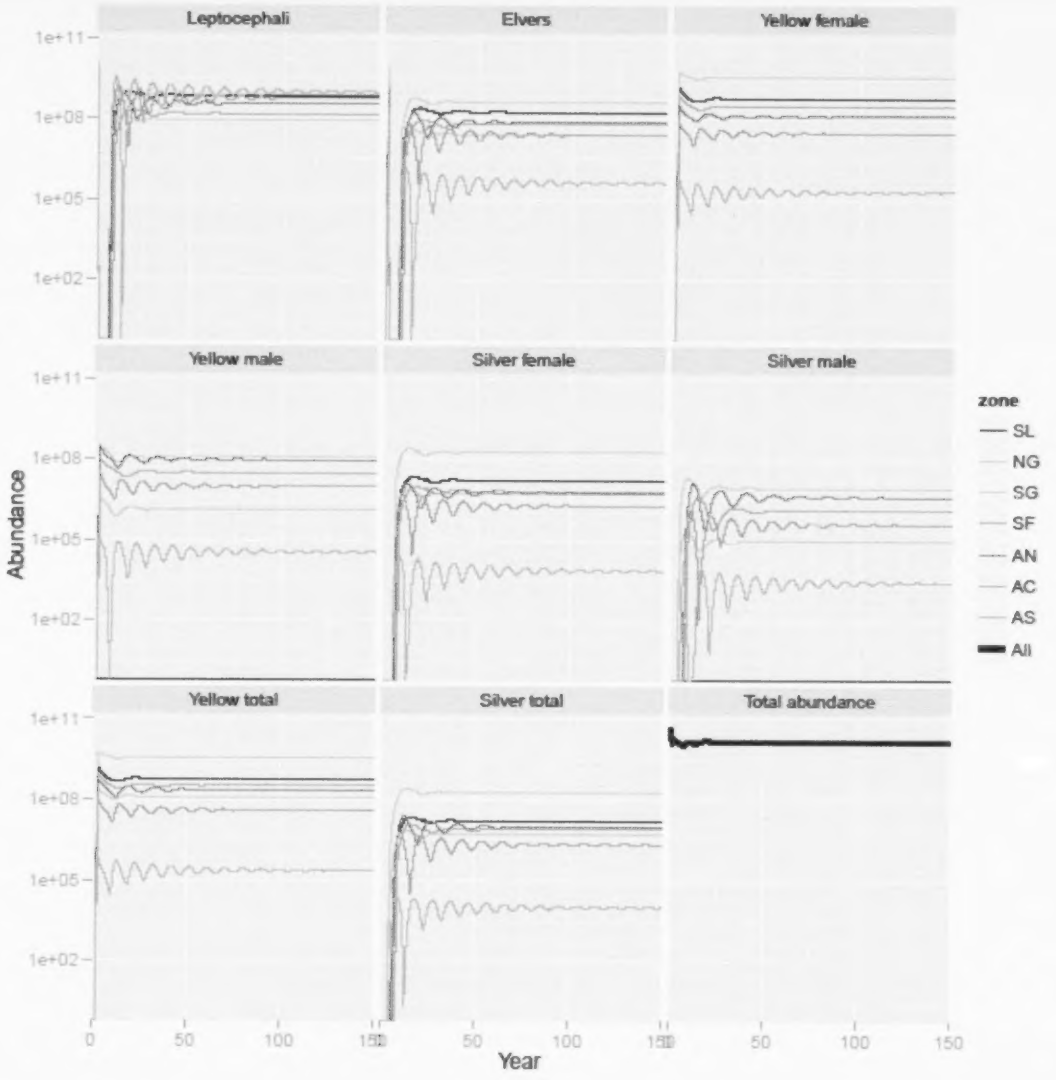

Figure 14. Projected population abundance (log scale) within each RPA zone and overall (All) by life stage assuming stationary rates under the full maternal effects (ME; d_m = 1) hypothesis.

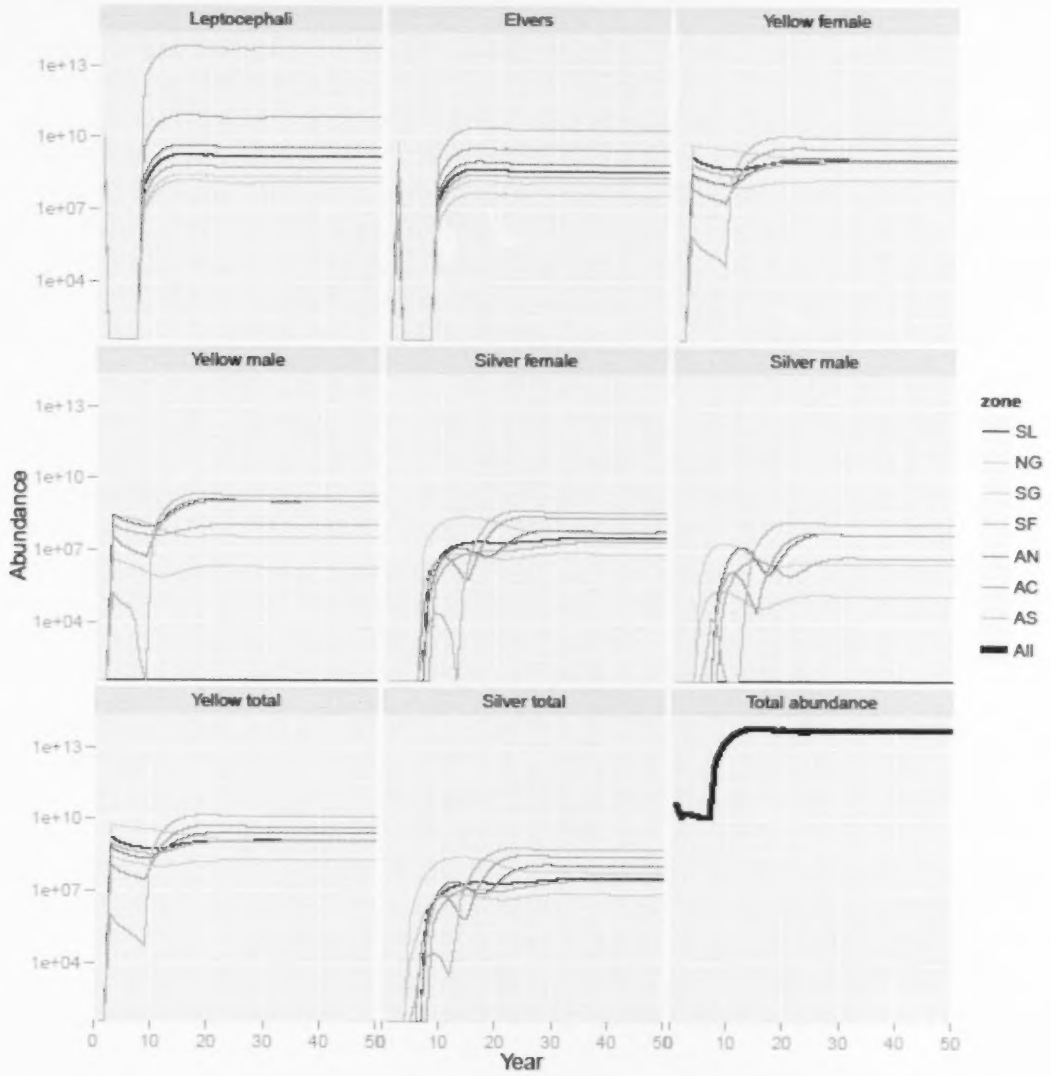

Figure 15. Projected population abundance (log scale) within each RPA zone and overall (All) by life stage assuming stationary rates under the full water attraction (WA; $d_m = 0$) hypothesis.

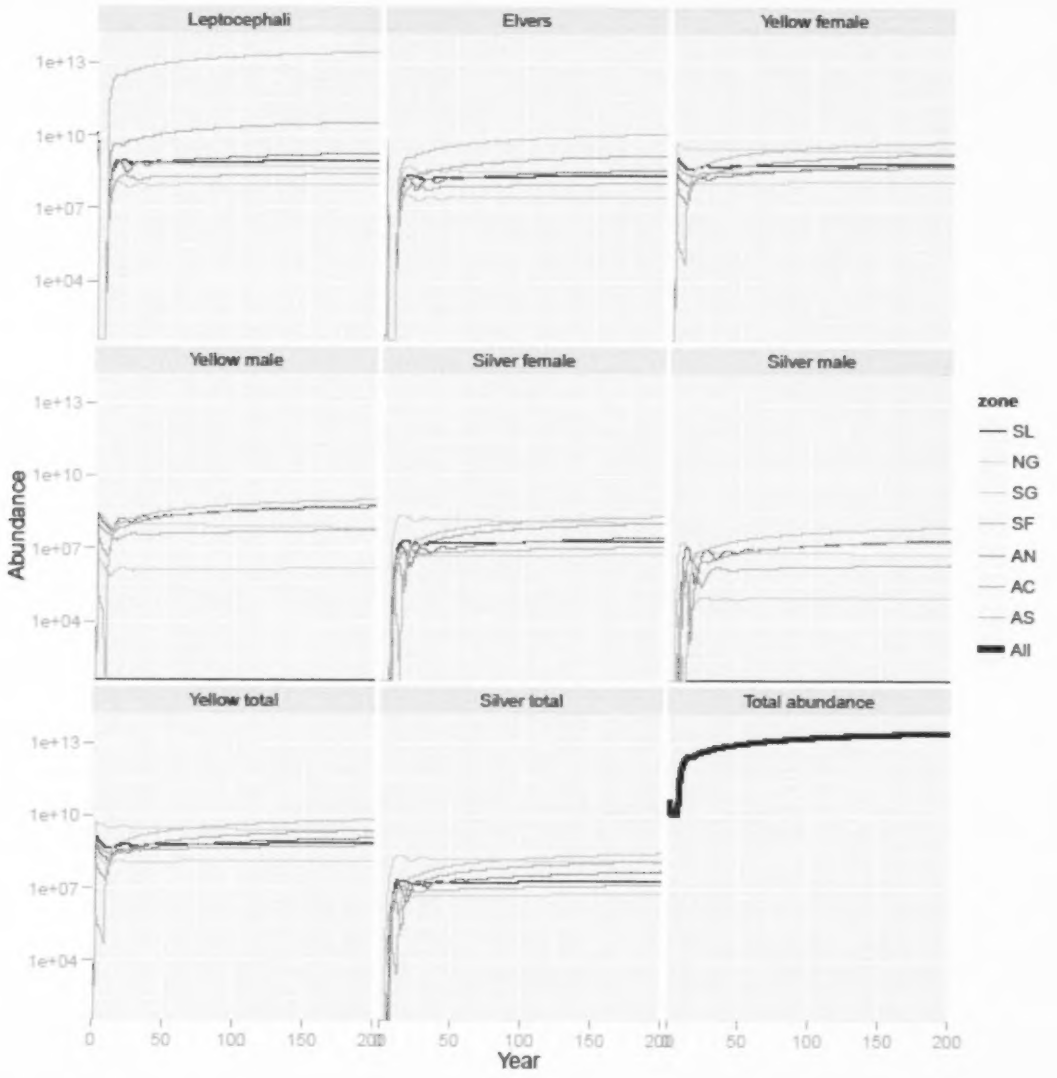

Figure 16. Projected population abundance (log scale) within each RPA zone and overall (All) by life stage assuming stationary rates under the hybrid maternal / water attraction distribution (HWA; $d_m = 0.95$) hypothesis. The population abundances are not yet at equilibrium due to transient dynamics.

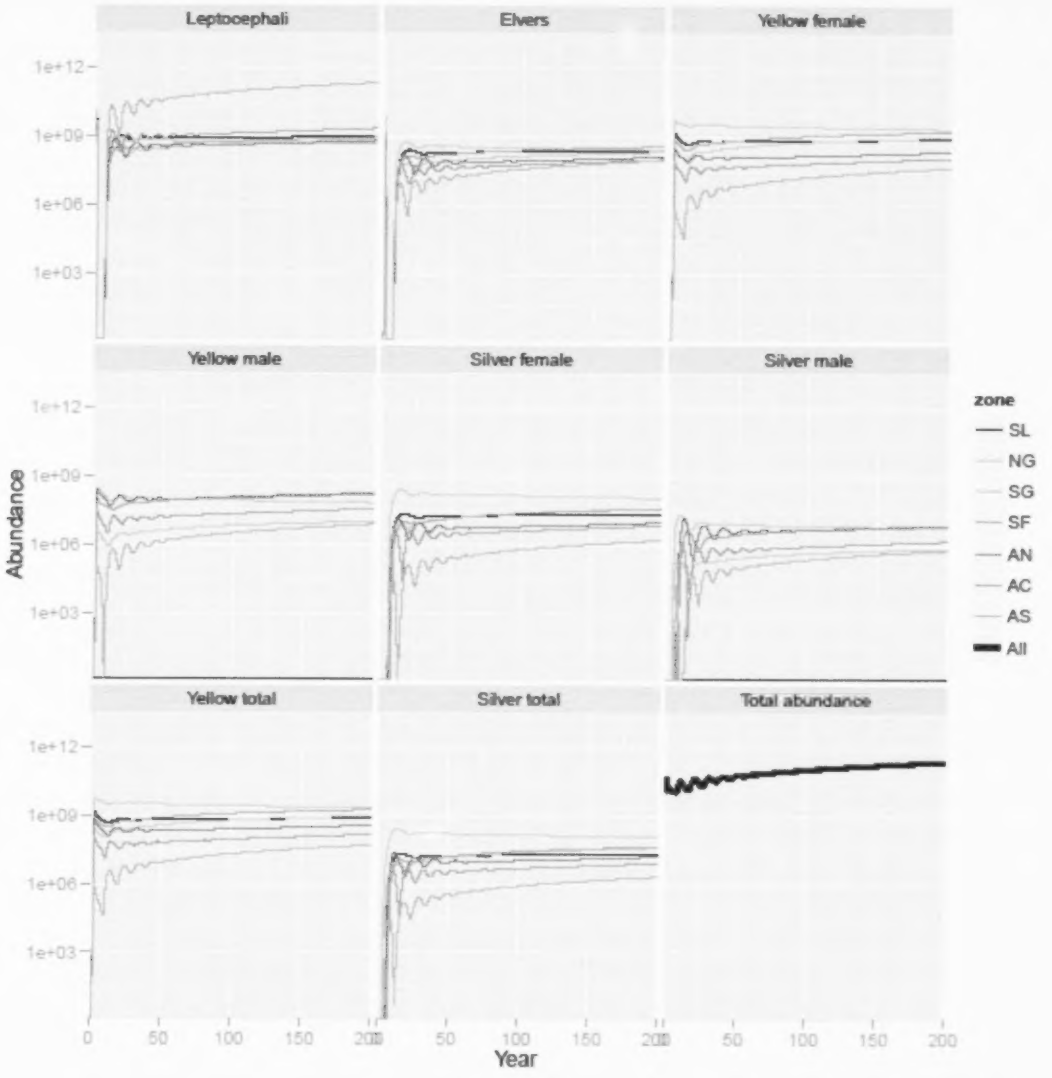

Figure 17. Projected population abundance (log scale) within each RPA zone and overall (All) assuming equilibrium under the hybrid maternal / nearest neighbour straying (HNN; $d_m = 0.95$) hypothesis. The population abundances are not yet at equilibrium due to transient dynamics.

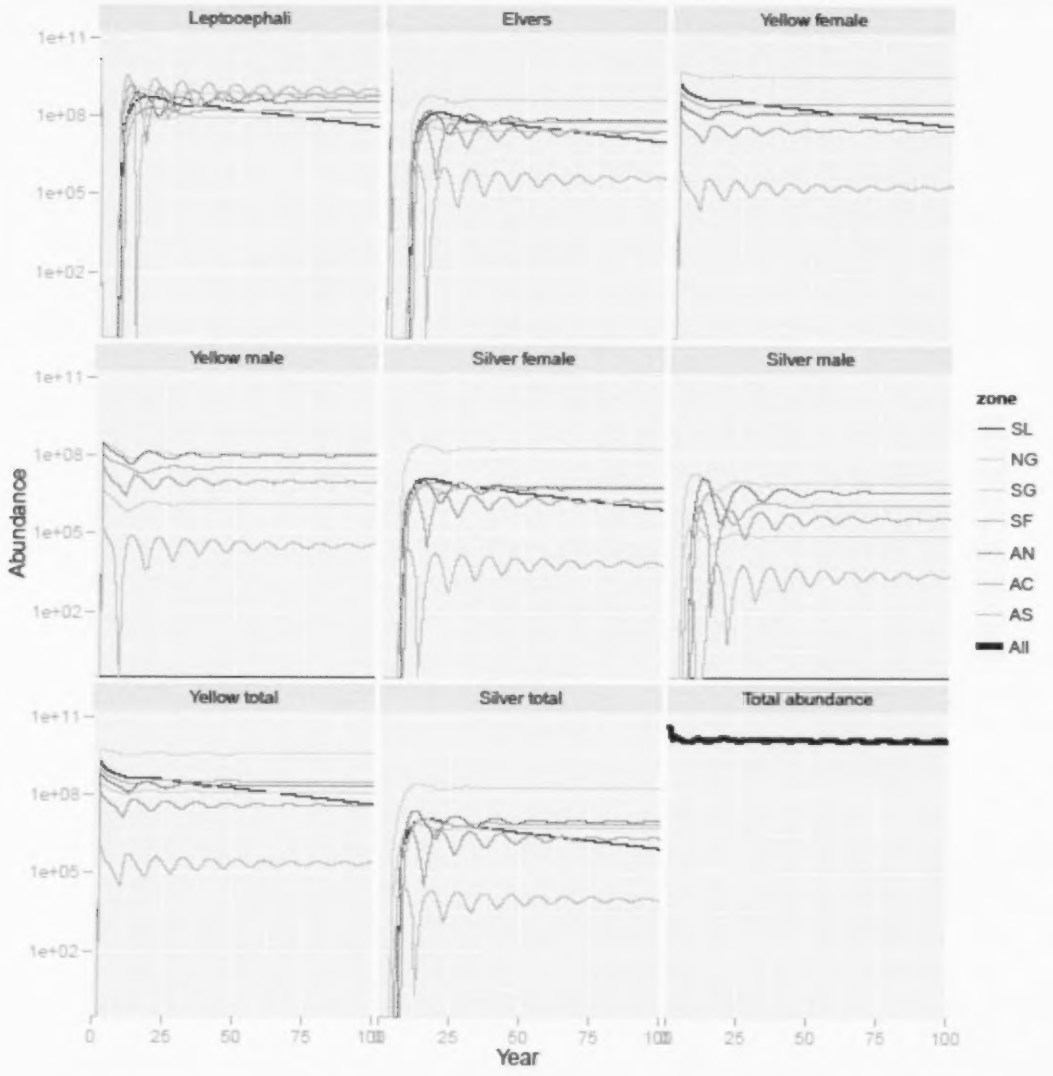

Figure 18. Projected population abundance (log scale) within each RPA zone and overall (All) assuming full maternal effects (ME; $d_m = 1$) hypothesis and equilibrium in all zones except SL where fishing mortality = 0.4 and turbine mortality = 0.17. Figure shows long term decline in SL ($\lambda_{SL} = 0.97$) and stability in remaining zones. Note that decline is exponential but does not appear so due to the log scale.

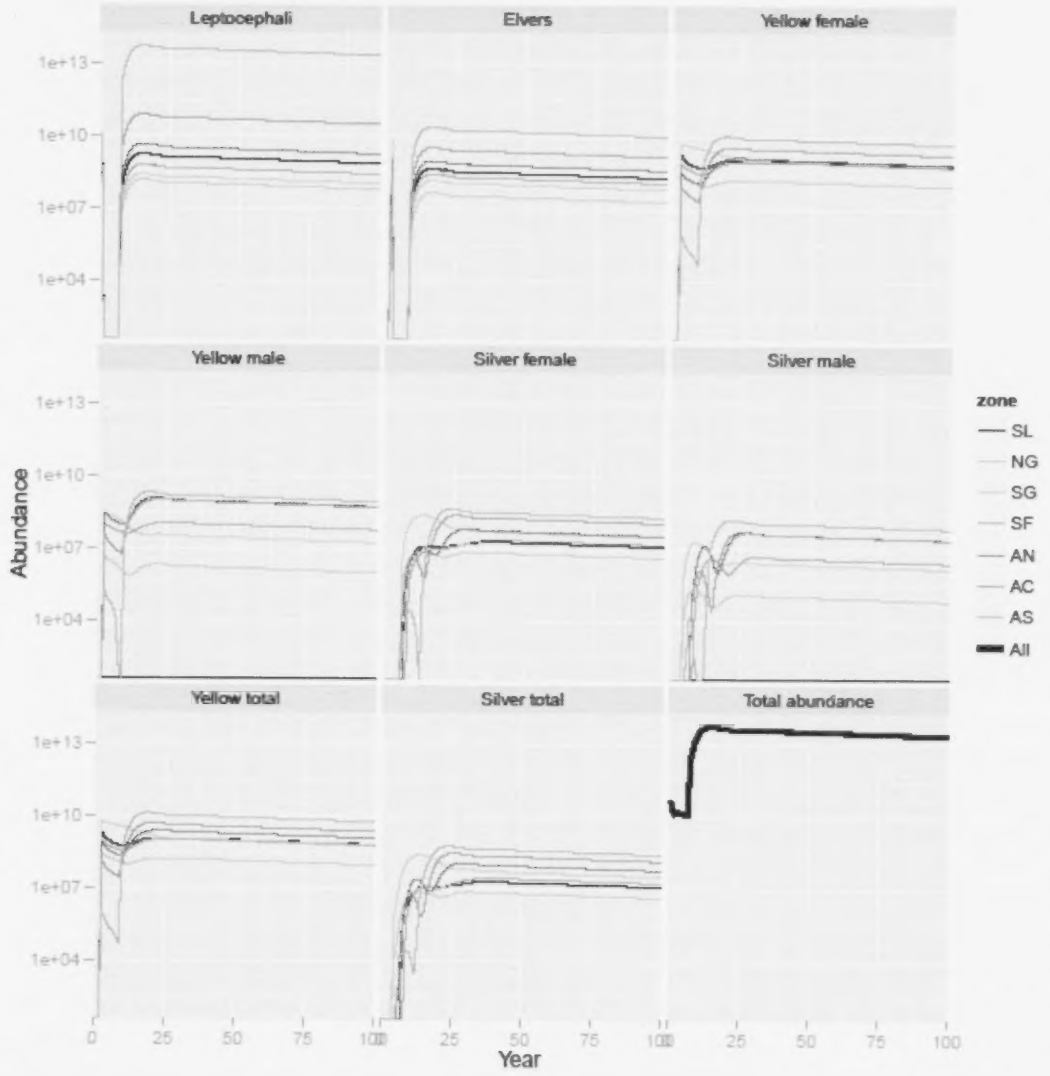

Figure 19. Projected population abundance (log scale) within each RPA zone and overall (All) assuming full water attraction distribution (WA; $d_m = 0$) hypothesis and equilibrium in all zones except SL where fishing mortality = 0.4 and turbine mortality = 0.17. Figure shows long term decline of $\lambda = 0.992$. Note that decline is exponential but does not appear so due to the log scale.

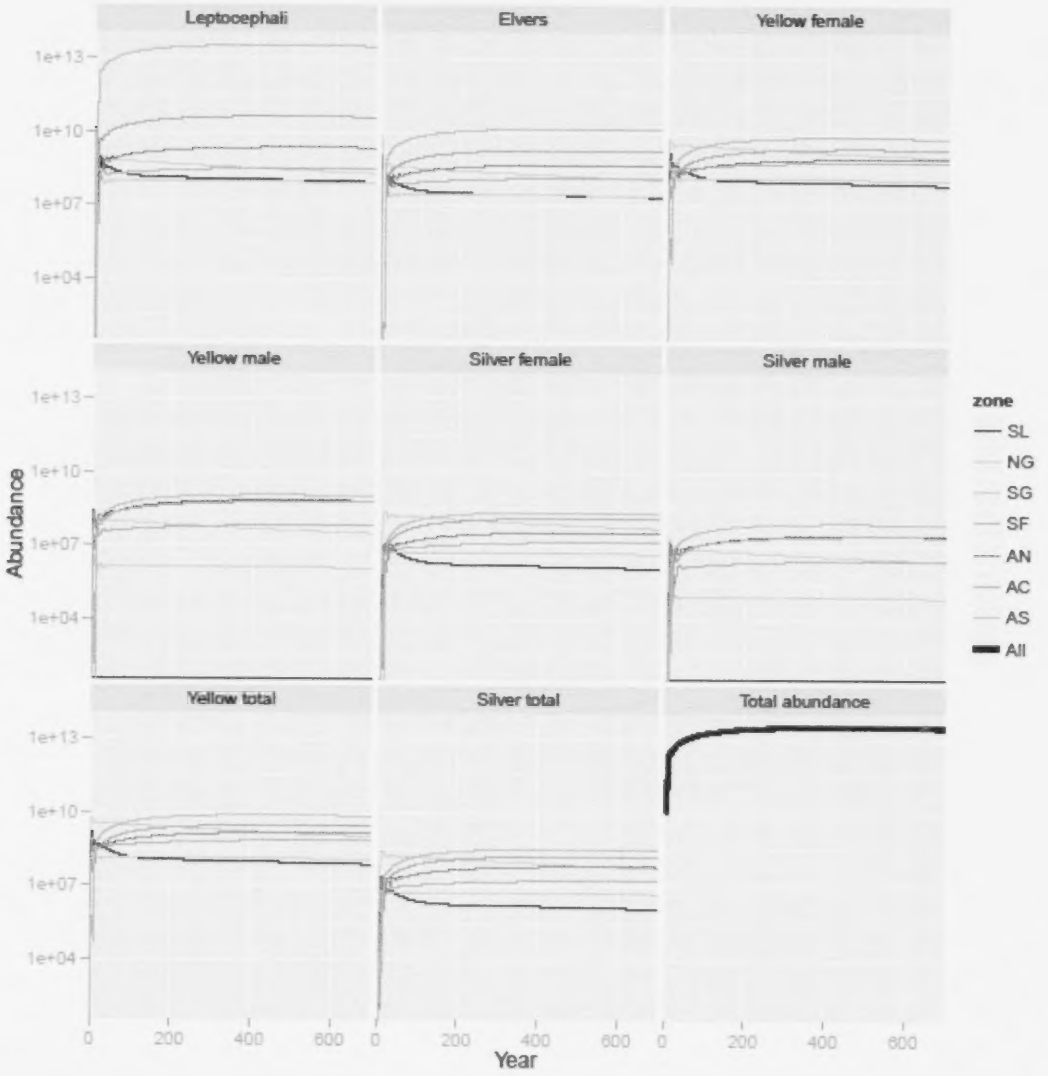

Figure 20. Projected population abundance (log scale) within each RPA zone and overall (All) assuming strong maternal effects and weak water attraction (HWA; d_m = 0.95) hypothesis and equilibrium in all zones except SL where fishing mortality = 0.4 and turbine mortality = 0.17. Transient dynamics show temporary growth in some zones but eventual long term slow population decline(λ = 0.999) is not observed in this timeframe.

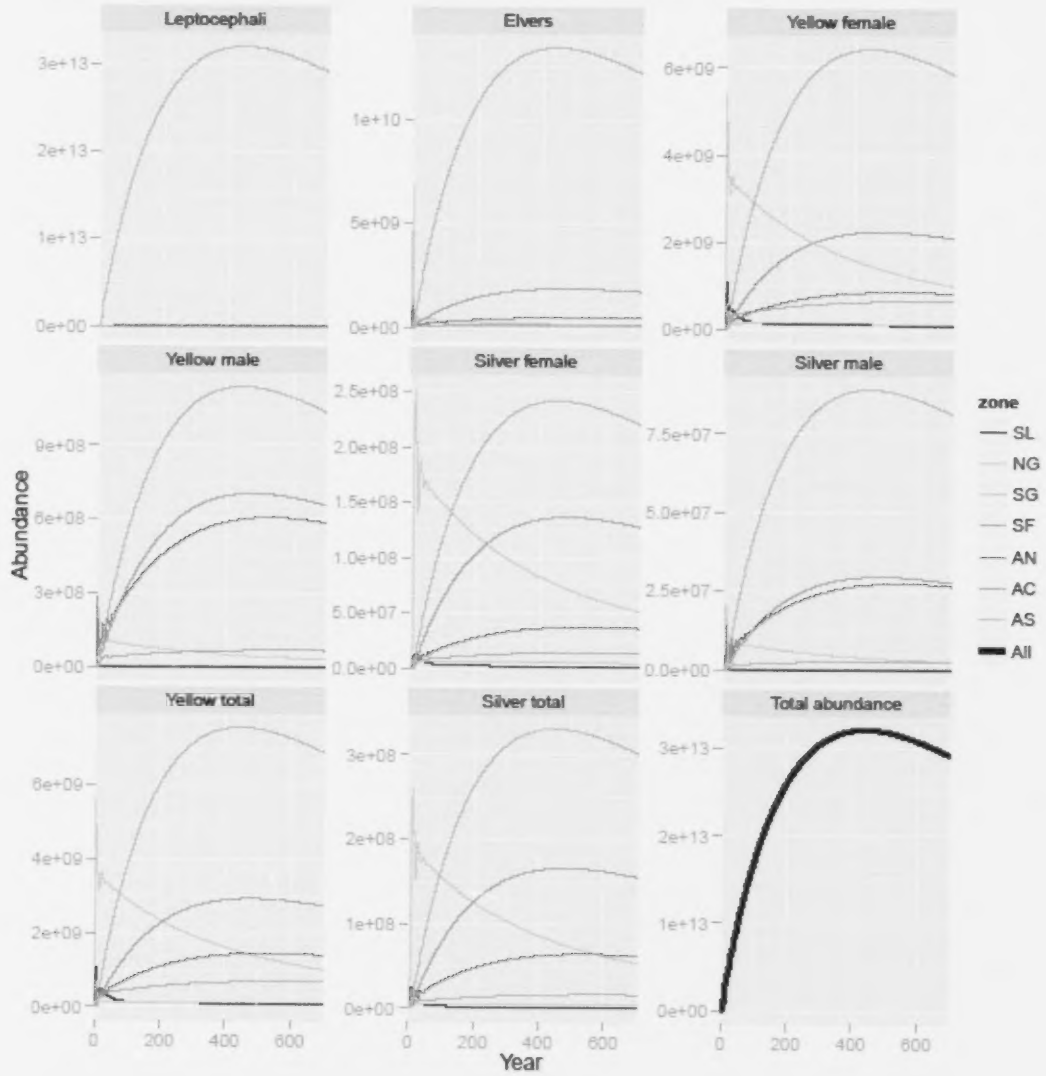

Figure 21. Projected population abundance within each RPA zone and overall (All) with same assumptions as Figure 20, with y-axis in natural scale.

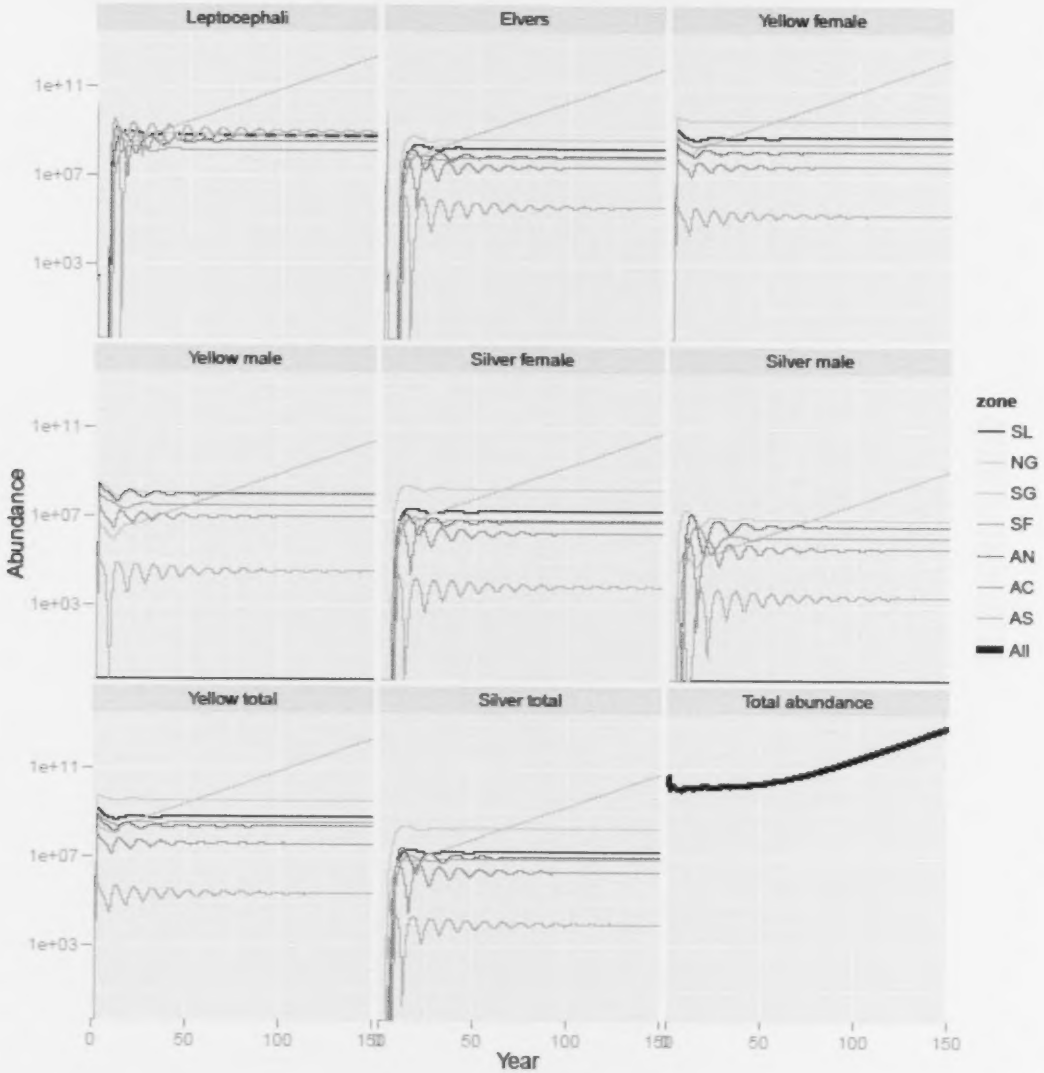

Figure 22. Projected population abundance (log scale) within each RPA zone and overall (All) assuming full maternal effects (ME; $d_m = 1$) hypothesis and stationary rates in all zones except SG, which is doubling every 10 years ($\lambda_{SG} = 1.07$). Note that growth is exponential but does not appear so due to the log scale.

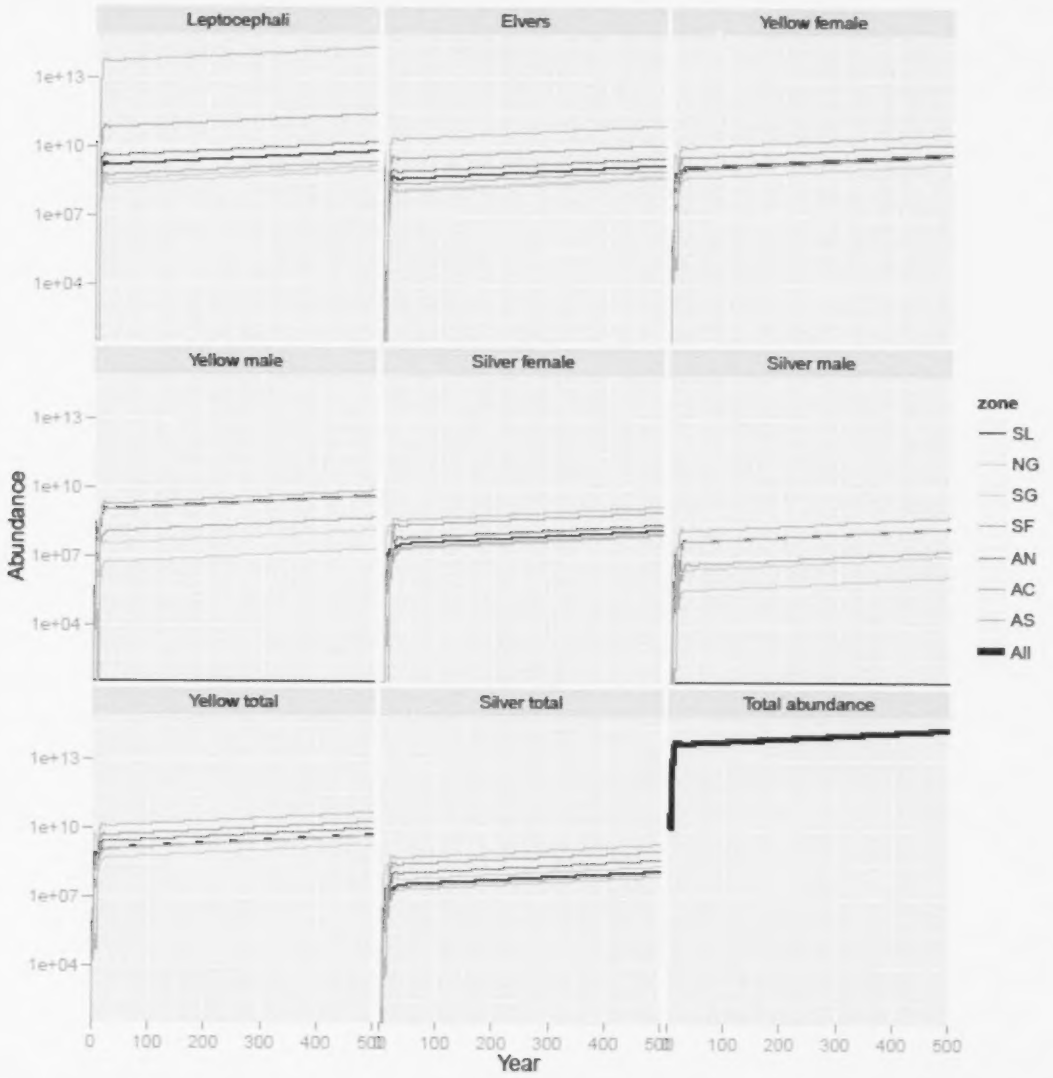

Figure 23. Projected population abundance (log scale) within each RPA zone and overall (All) assuming full water attraction distribution (WA; $d_m = 0$) hypothesis and stationary rates in all zones except SG, which is growing. Figure shows long term growth of $\lambda = 1.003$ in all zones. Note that growth is exponential but does not appear so due to the log scale.

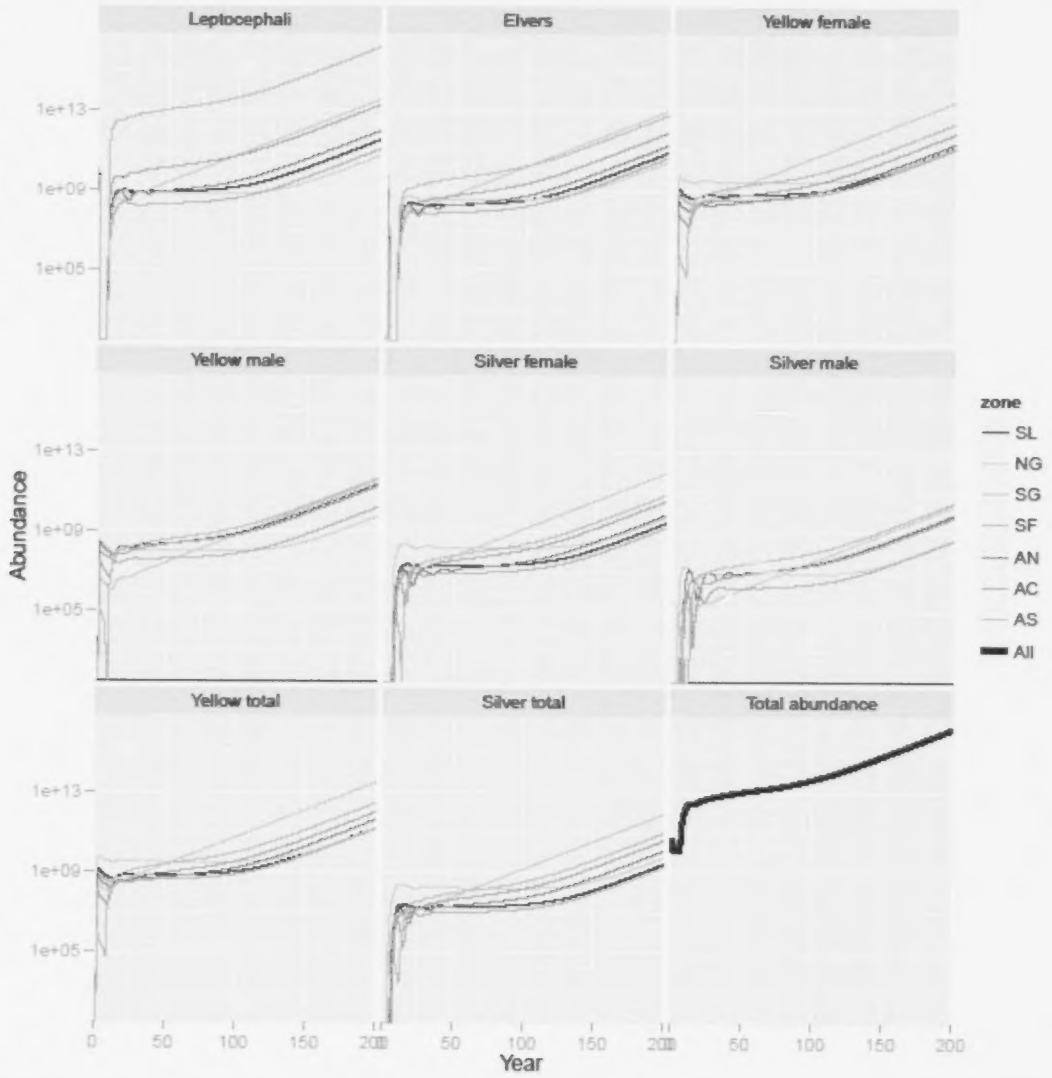

Figure 24. Projected population abundance (log scale) within each RPA zone and overall (All) assuming hybrid maternal effects with weak water attraction (HWA; $d_m = 0.95$) hypothesis and stationary rates in all zones except SG, which is growing. Figure shows long term population growth of $\lambda = 1.066$ in all zones after significant transient dynamics.

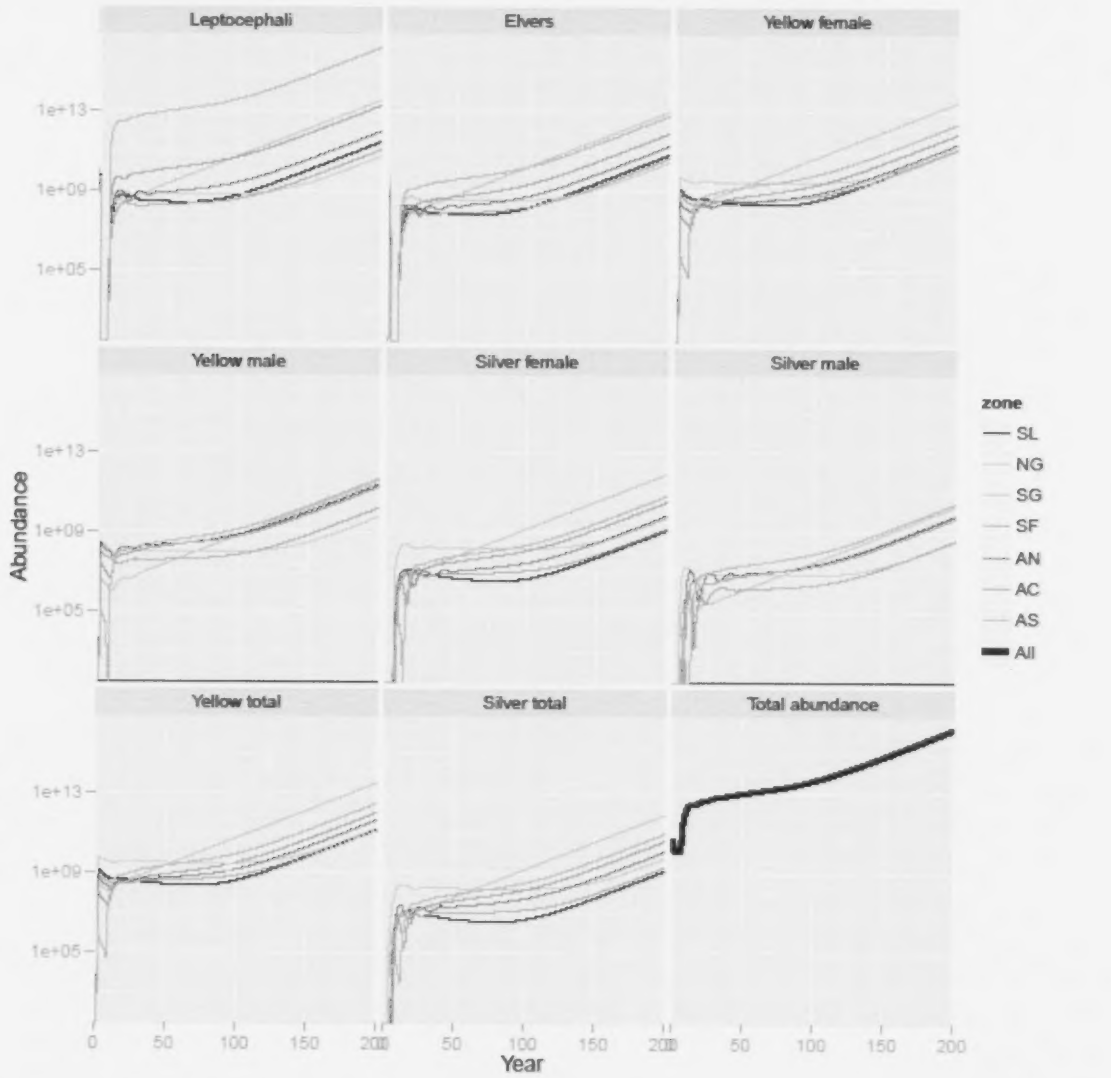

Figure 25. Projected population abundance (log scale) within each RPA zone and overall (All) assuming hybrid maternal affects with weak water attraction (d_m = 0.95) hypothesis and stationary rates in all zones except SG, which is growing, and SL, which is in decline (MF_{SL} = 0.4; MT_{SL} = 0.17). Figure shows temporary decline in SL with long term growth of λ = 1.066 in all zones.

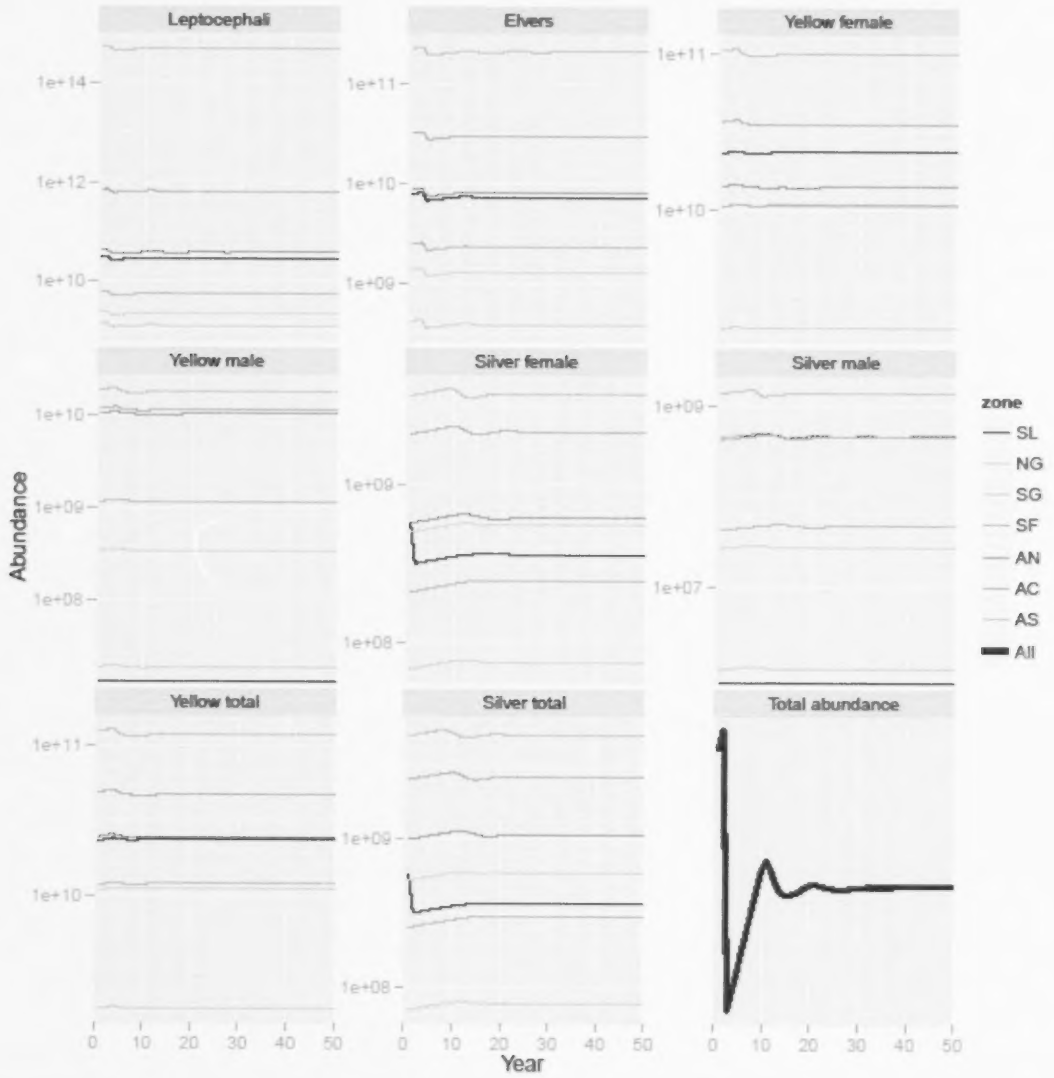

Figure 26. Projected population abundance (log scale) within each RPA zone and overall (All) assuming full water attraction distribution (WA; $d_m = 0$) hypothesis and stationary rates in all zones. The initial population abundance is set to the stable stage distribution for the growing SL zone.

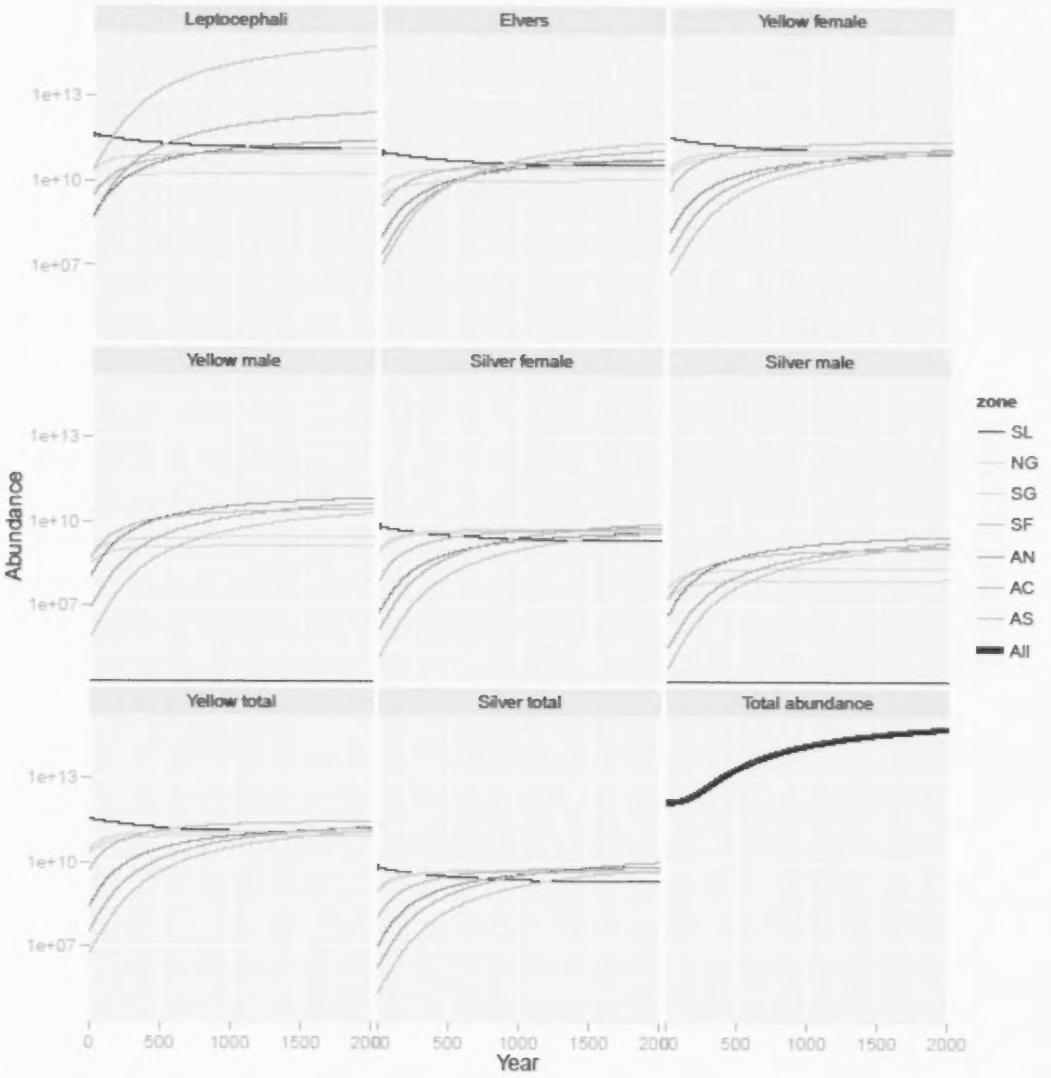

Figure 27. Projected population abundance (log scale) within each RPA zone and overall (All) assuming hybrid maternal effects with nearest neighbour straying (HNN; d_m = 0.95) hypothesis and stationary rates in all zones. The initial population abundance is set to the stable stage distribution for the growing SL zone.

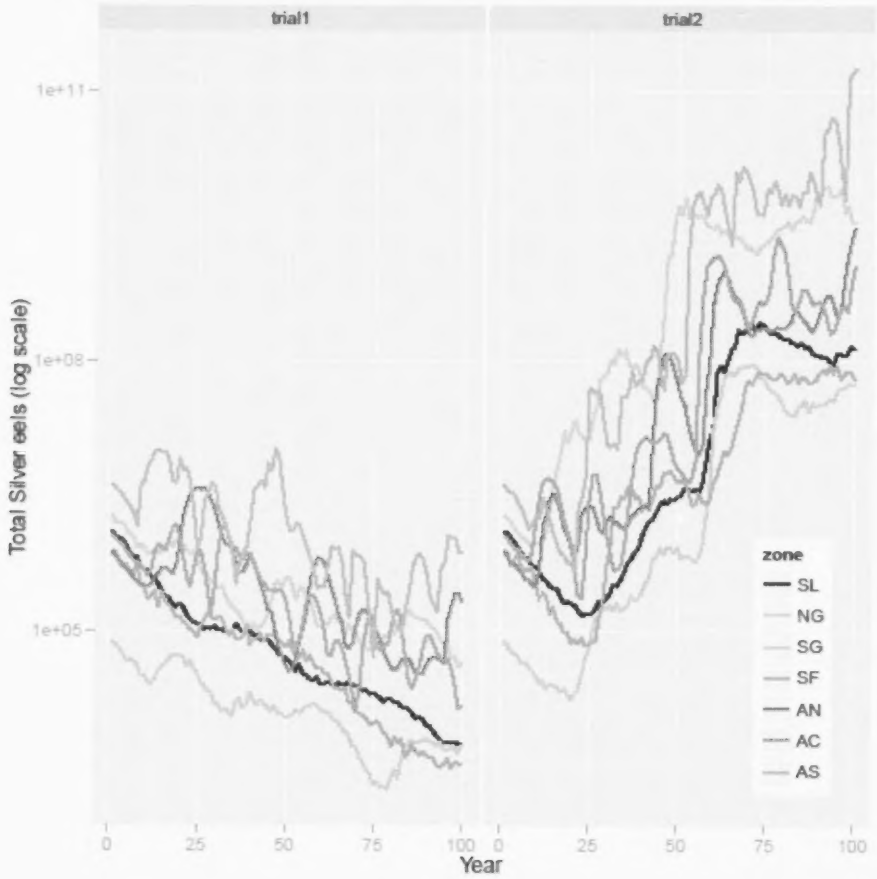

Figure 28. Two example population trajectories (log scale) of total silver eels (by RPA zone) from stochastic simulations. Vital rates for both trials were drawn from the same distributions and the full water attraction distribution hypothesis was assumed.

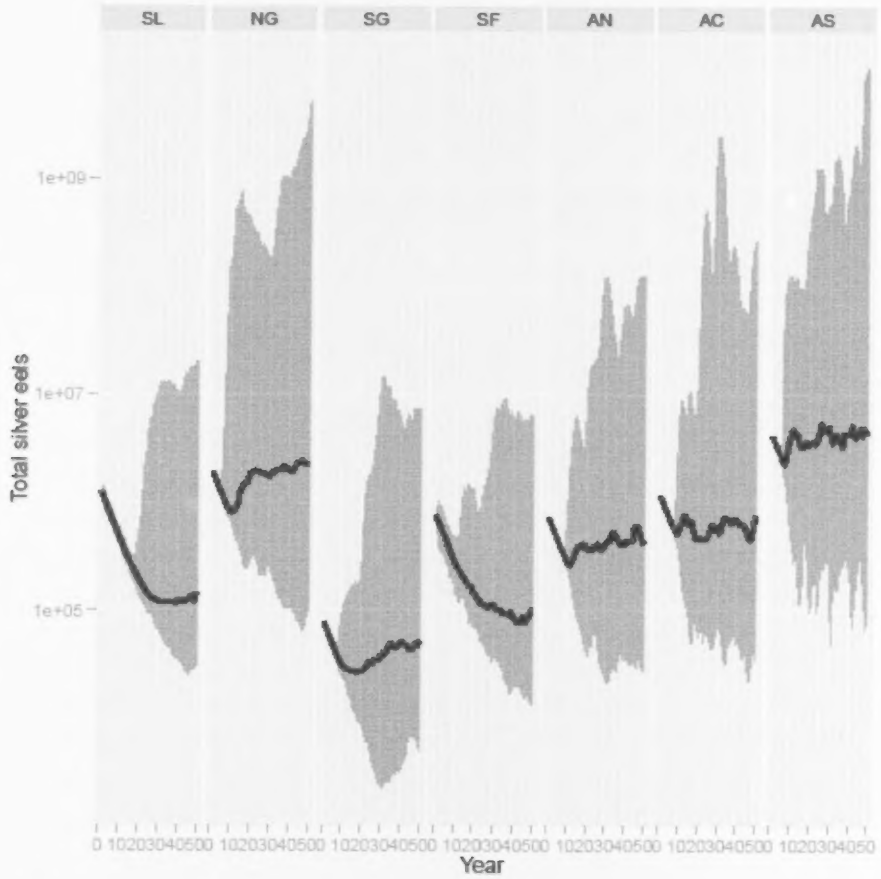

Figure 29. Population trajectories (log scale) of total silver eels (by zone) from 100 stochastic simulations. Median (black line) and range (gray) of all trials are shown for the full water attraction distribution hypothesis.

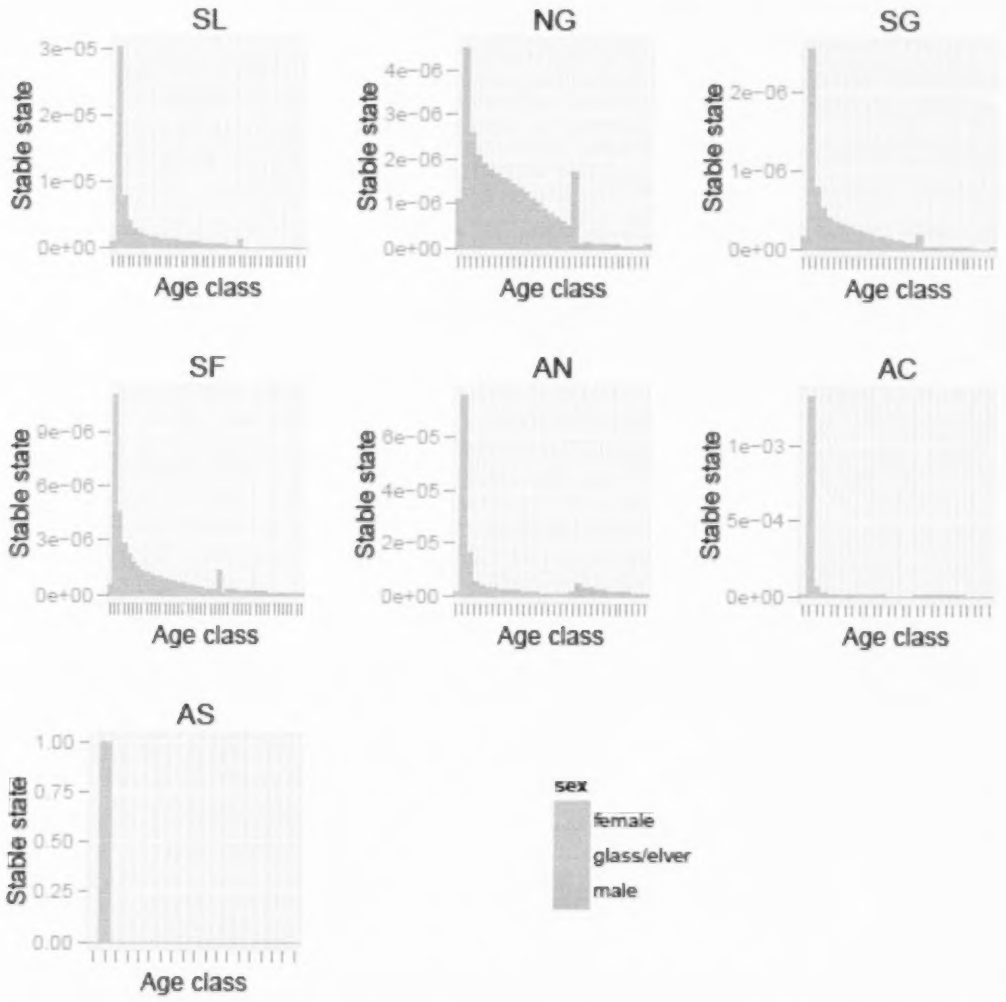

Figure 30. Stable stage distribution for all age classes, by RPA zone, assuming water attraction or hybrid maternal / water attraction distribution (WA, HWA; $d_m < 1$) hypotheses and stationary rates. From left to right in each zone, age classes are: silver females, leptocephali, elvers, yellow females, silver males, yellow males.

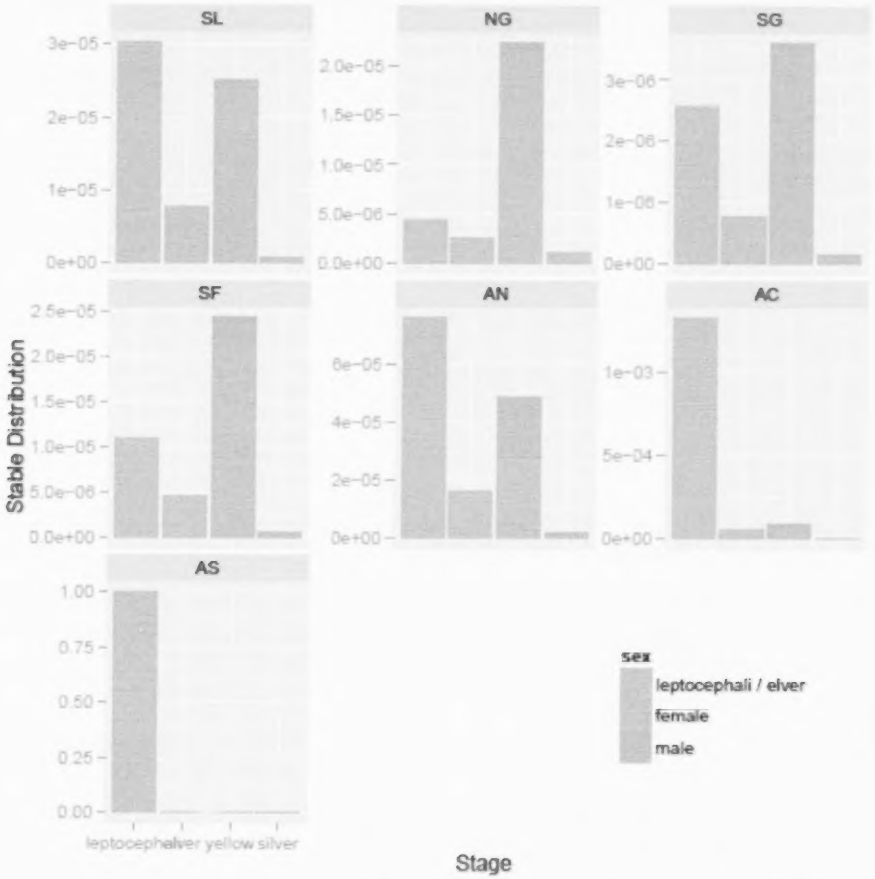

Figure 31. Stable stage distribution, assuming water attraction or hybrid maternal / water attraction distribution hypotheses, and stationary rates; summarized by stage (leptocephali, elver, yellow, silver), sex (male, female, undetermined), by RPA zone for comparison within each zone.

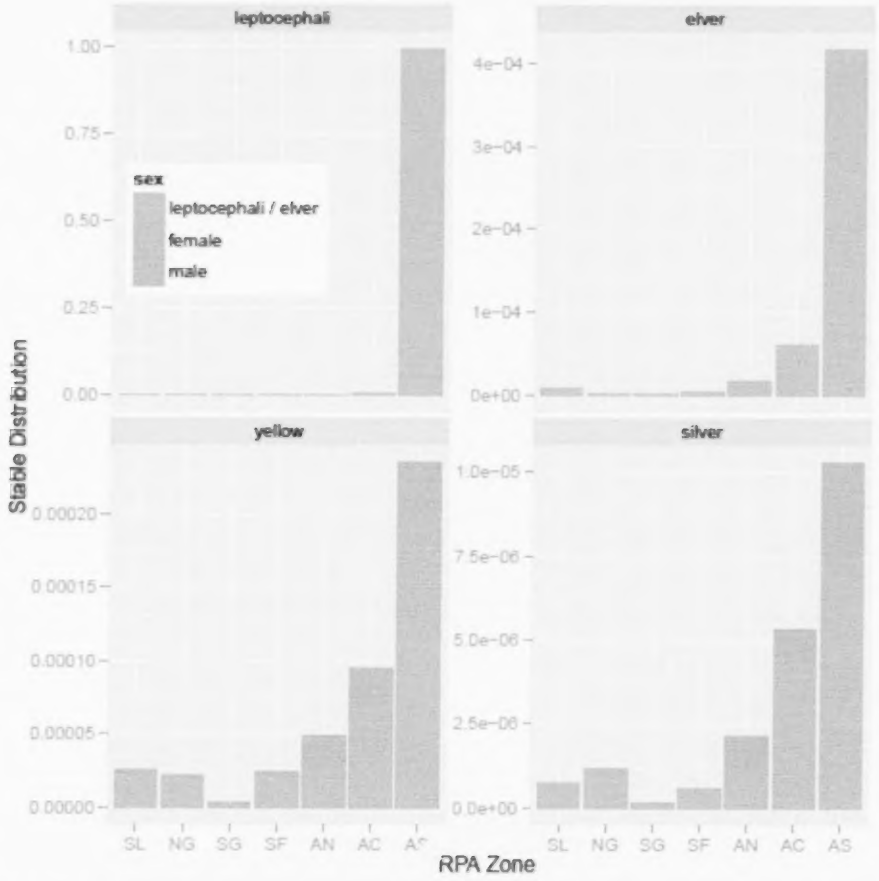

Figure 32. Stable stage distribution, assuming water attraction or hybrid maternal / water attraction distribution hypotheses and stationary rates; summarized by stage (leptocephali, elver, yellow, silver), sex (male, female, undetermined), and RPA zone for comparison across zones.

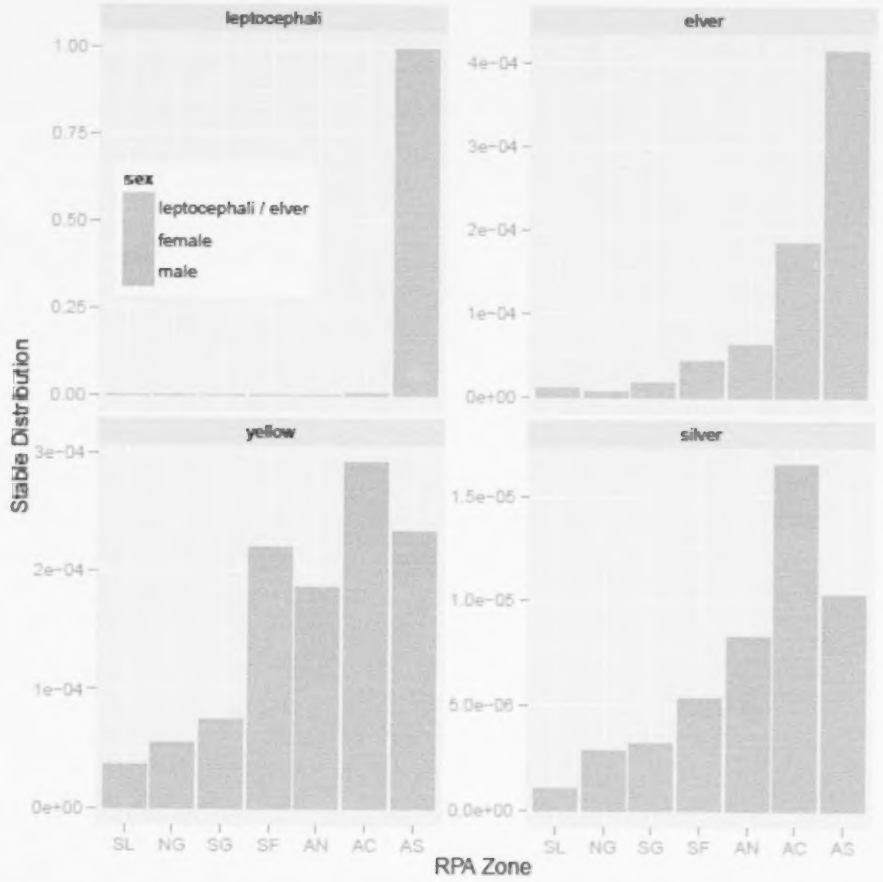

Figure 33. Stable stage distribution by life stage among RPA zones, assuming hybrid maternal / nearest neighbour distribution hypotheses and stationary rates; summarized by stage (leptocephali, elver, yellow, silver), sex (male, female, undetermined), for comparison across zones.

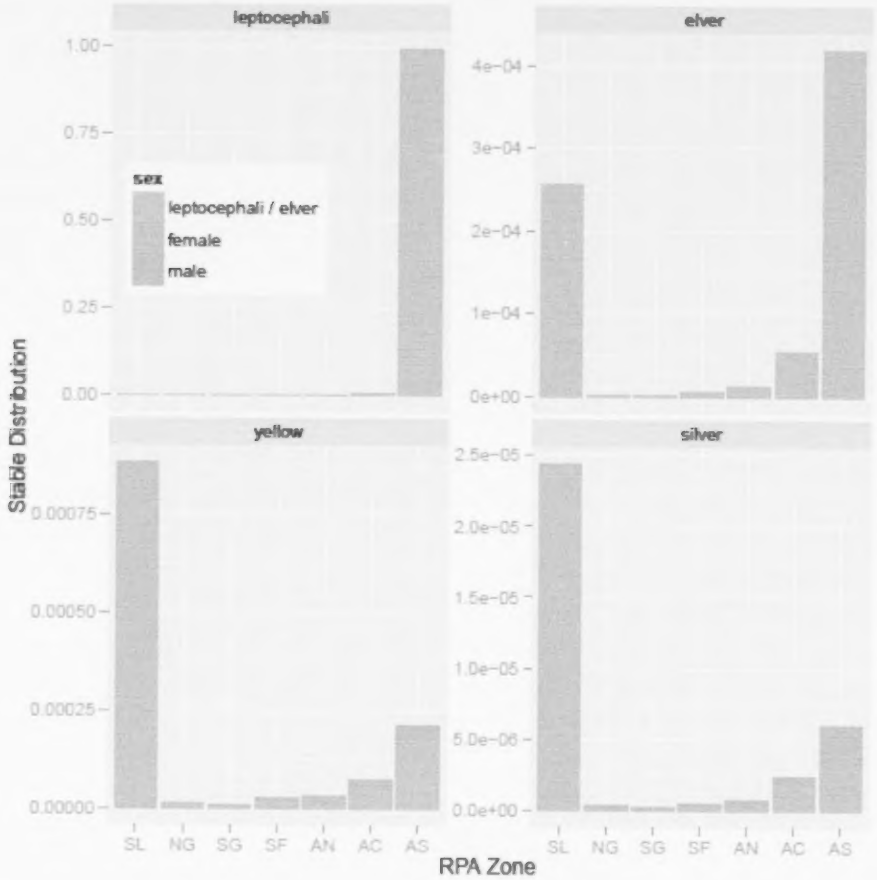

Figure 34. Stable stage distribution by life stage among RPA zones, assuming hybrid maternal / water attraction distribution (d_m = 0.95) hypothesis and decline due to fishing; summarized by stage (leptocephali, elver, yellow, silver), and sex (male, female, undetermined).

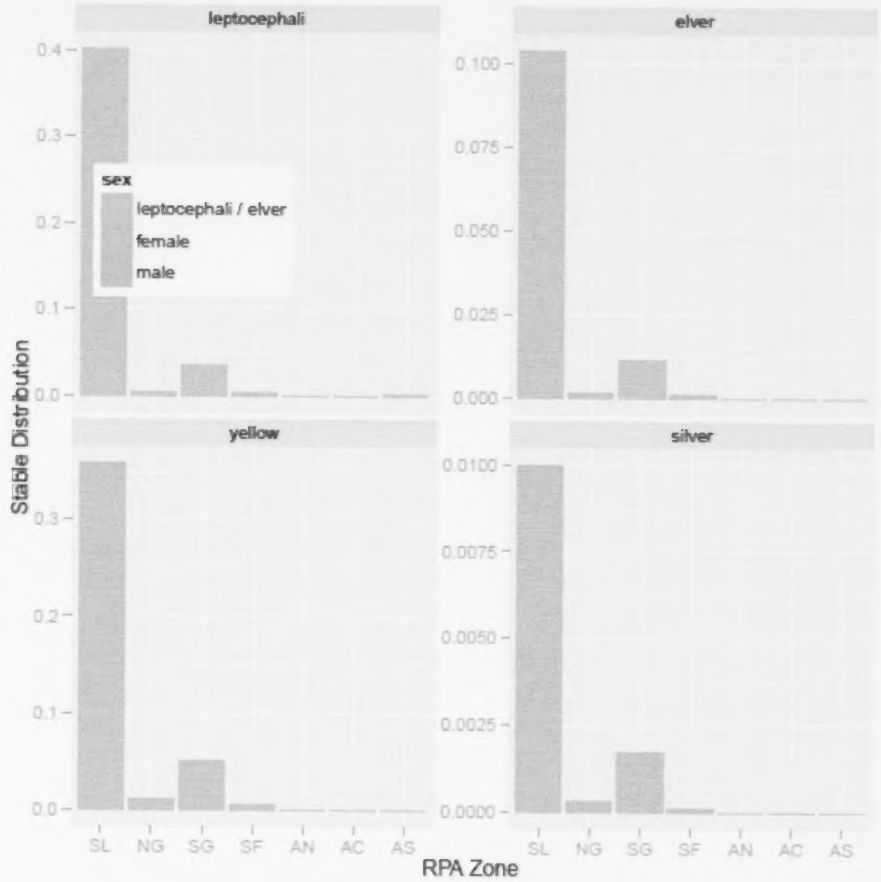

Figure 35. Stable stage distribution by life stage among RPA zones, assuming hybrid maternal / nearest neighbour distribution hypothesis (d_m = 0.95) and decline due to fishing; summarized by stage (leptocephali, elver, yellow, silver), and sex (male, female, undetermined).